VOLUME LXIV NUMBER 5

THE
BOTANICAL GAZETTE

NOVEMBER 1917

FOOTHILLS VEGETATION IN THE COLORADO FRONT RANGE

CONTRIBUTION FROM THE HULL BOTANICAL LABORATORY 237

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(WITH EIGHT FIGURES)

The coniferous forests of the Rocky Mountains are fairly well known; the other plant associations have been little studied. In the present account descriptions are given of typical representations of the plant communities of the foothills zone. The area is confined to the eastern slope of the Rockies in Colorado. By the foothills zone is meant the lower elevations, from the plains at 5000–6000 ft. to the middle slopes at 7500–8000 ft. The vegetation zones of the Colorado mountains have been characterized by RAMALEY (10). A large part of the field study has been made in the area just west of Boulder, during three years' residence at the University of Colorado; the other parts of the region have been studied on numerous visits, chiefly to stations at or near the mountain-front, from the Big Thompson River as far south as Raton, New Mexico. This article is the second of a series dealing with the vegetation and plant geography of the eastern mountain-front in Colorado. The first account (24) is of the plains and prairie associations of the region. The writer is indebted to Professor FRANCIS RAMALEY for many kindnesses and for help in different ways.

Grassland in the Rocky Mountains has a much more important rôle than is usually accredited to it, particularly in the lower slopes.

It is perhaps the conspicuousness of the trees, especially in distant views and in profiles of slopes (fig. 8), which gives the common but not wholly true impression that the foothills are generally forested with conifers. The rock pine, the most generally distributed conifer of the region, forms relatively few and scattered true forests; it usually grows in very open formation, in mixture with the grassland which covers most of the surface. The general aspect of the vegetation is that of an open growth of grassland and scattered pines over a dry and partly bare upland of granitic hills. Semi-mesophytic and mesophytic communities, of both herbaceous and woody plants, occur; but only locally, in moister or more sheltered ravines and canyon-bottoms. The vegetation complex of the mountain-front is a modification of that of the foothills, but is less simple in composition.

Environmental conditions

The Front Range in Colorado is an up-arched and dissected plateau of crystalline rocks, the tops of most of the hills forming the remains of a peneplaned surface; scattered higher mountains represent monadnocks surmounting the former general level. The eastern part of the plateau slopes gently toward the plains, the sedimentary strata of which are here upturned against the granitic rocks, forming sloping crags on the outer face of the foothills, or hogback ridges separated from the hills by north-south valleys. The physical geography of the Front Range is described by DAVIS (5). It is with the lower, more easterly part of the granitic plateau and with the more irregular country of the mountain-front that this study has to do.

The climate of the foothill region is dry, though not enough so to be called semi-arid, like that of the plains. Rainfall at the mountain-front is from about 15 to 18 inches average for the year; higher in the northern part of the state and on the elevated Platte-Arkansas divide, lower south of the Arkansas River. The upper foothills receive about 18–20 inches. Annual variation of rainfall is considerable. Most of the rain comes during the growing season. At Boulder, and in the northern foothills generally, April and May are the rainiest months; in the southern foothills the earlier part of the summer is drier than later. This, with higher summer

temperatures and probably greater insolation, gives a drier aspect to the southern foothills; pinyons are abundant, instead of rock pine, as in the northern part of the state. Mean annual temperatures in the foothills vary from 40 to 50° F.; mean summer temperatures 60 to 70° (ROBBINS 17). Evaporating power of the air is great, though much less than on the plains. Local variations in atmospheric conditions, due to surface configuration, are considerable. Insolation is much greater on summits and south-facing slopes than on north-facing slopes or in ravines. The drying winds are usually from the west, and their effects are greatest on summits and the flatter uplands.

Local and topographic factors are extremely and very locally variable. Position with reference to surroundings, and slope, its amount and direction, may perhaps be called the two master factors of the topographic complex. Slope and position are most important in determining conditions of soil deposition or removal (consequently depth and texture of the soil); conditions of absorption and run-off, drainage, or seepage from above, or possible seepage from snowdrifts; presence or absence of plant remains, which may contribute humus, or locally form a mulch (pine needles); and conditions of exposure to sun and wind with its attendant effects. The granitic hills in general (fig. 1) are in an early-mature stage of topographic development (for a mountain region of resistant rocks); the side-slope profiles are nearly straight, with comparatively little detritus covering the bottom of slopes; the tops of the hills are usually rounded, and hardly more subject to erosion than the sides. In general, the foothills are so well drained that bogs, marshy flats, and moist-soil meadow areas are infrequent, even in canyon-bottoms. Hilltops and side-slopes are covered, usually thinly, with rock-débris or with decomposed granite soils, varying in texture from coarse gravelly material of angular fragments[1] to fine black loamy humus. Wide dikes and occasional outcrops of more resistant rock have only a little soil, in joints and crevices, hardly any elsewhere.

[1] The writer has not been able to find a distinctive name for this coarse angular débris resulting from decomposition of granite; it is not gravel in the sense the word usually implies; in this article it will be called "granite-gravel."

Texture of soil in its influence on water relations is probably the most important soil factor in the foothills, so far as local distribution of plants is concerned. Especially interesting are some of the features of mixed soils, in which fragments of greatly different sizes are intermingled. Rocks of all sizes may occur on the surface, or buried among finer fragments as rock-débris of detrital slopes. Where the large fragments are imbedded beneath the surface in fine soil, the water content of the latter appears to be increased.

FIG. 1.—General view in foothills, looking westward to snowy range-crest; foreground a north slope; general vegetation grassland with scattered pines; southwest of Boulder, 7200 ft.

Where the large rocks are exposed at the surface, moisture conditions appear to be more favorable immediately beside and under them, so that comparatively mesophytic plants are seen growing in mixture with xerophytes, the former always growing beside or from under the surface rocks. This effect will be noticed in the lists of species; many plants are found in both xerophytic and mesophytic assemblages.

The more frequently recurring combinations of topographic and atmospheric factors which form effectively different local environments for plants may be viewed in the synopsis which follows. It is intended to apply only to the foothills proper; a number of situations of the mountain-front belt cannot be included herein.

CLASSIFICATION OF FOOTHILLS HABITATS

Xerophytic habitats (the general condition of summits and side-slopes)
- Rocky habitats
  - Craggy summits and rock-walls (see figs. 2, 3)
  - Rock-strewn detritus slopes
  - Rock-talus, usually less stable than preceding
- "Granite-gravel" habitats
  - Compacted granite-gravel floors and side-slopes (see fig. 3)
  - Loose granite-gravel floors, washes, and talus (= gravel slides)
- Fine-soil habitats
  - Mixed-soil floors and detritus-slopes (fine soil with imbedded and superficial rock fragments of various sizes)
  - Fine-soil floors and detritus-slopes (infrequent)

Less xerophytic habitats (valleys and steep slopes, etc., relatively local)
- Less xerophytic side-slopes (mostly north-facing, usually of considerable gradient, and best developed in valleys)
- Mesophytic ravine habitats
  - Narrow ravines (best developed in small side-canyons, especially on the south side of eastward-flowing main streams)
  - Canyon-bottoms (the wider bottoms of the larger canyons are sometimes, however, exposed and xerophytic)
  - Seepage and dripping areas (infrequent and small)
  - Stream-side habitats (with usually constant supply of soil moisture, but widely varying atmospheric conditions)

Synopsis of plant associations

The following synopsis is aimed to give in perspective the distinguishing characters of the plant communities of the foothill region. It is based upon whatever features of the particular community seem most distinctive and appropriate: growth-form, moisture relations, physiographic, geographic, and successional relations.

CLASSIFICATION OF FOOTHILLS ASSOCIATIONS

Associations generally primitive in character: the first vegetation of new or unfavorable habitats, usually in rocky or gravelly situations; vegetation open and sparse, generally xerophytic
- Plants lichens; on rock surfaces, either on craggy summits, knobs, and rock-walls, or on loose boulders ..... *Lichen associations*
- Plants spermatophytes, in rocky or detrital situations, soil of variously coarse texture
  - Dominant plants shrubs; of relatively local and temporary occurrence; frequent in areas recently denuded ..... *Sumac association*
  - Dominant plants herbaceous ..... *Foothills primitive grassland association*

Associations generally intermediate or established in character (usually subsequent to primitive associations, but often in habitats apparently little modified from the primitive condition); soil often of mixed or fine texture, or with considerable humus content; vegetation usually less open and sparse than in preceding

Typically developed in xerophytic or semi-xerophytic habitats, which are of general occurrence in the foothills region (these associations are consequently extensive)

Dominant plants evergreen trees; usually in rocky or coarse soil

Of relatively less xerophytic character; generally distributed in the foothills region ..... *Rock pine association*

Of relatively more xerophytic character; of lower and (east of the range-crest) more southerly distribution than preceding

Pinyon-cedar association

Dominant plants deciduous trees or large thicket-forming shrubs; of southerly distribution east of the range-crest; frequent in fine soil, and ranging into less xerophytic habitats ..... *Quercus association*

Dominant plants shrubs

Shrubs tall and loosely branched, occurring mostly at and near the mountain-front, in coarse or rocky soils ..... *Cercocarpus association*

Shrubs low, creeping and densely branched, occurring mostly in the foothills proper

Plants evergreen, of northerly distribution, more frequent in the higher foothills ..... *Arctostaphylos association*

Plants deciduous, of more southerly distribution, more frequent in the lower foothills ..... *Ceanothus association*

Dominant plants herbaceous; vegetation grassland, composed mostly of xerophytes

Dominant plants including plains short-grasses of surface-rooted habit; plant population large and diverse, *Foothills mixed grassland association*

Dominant plants mostly tufted bunch-grasses of deeper-rooted habit

Bunch-grass association

Typically developed in mesophytic or semi-mesophytic habitats (which are much less extensive in the foothills than xerophytic habitats, being represented chiefly on north slopes and in ravines and canyons)

Dominant plants evergreen trees ..... *Pseudotsuga association*

Dominant plants deciduous trees

Typically developed along stream margins in open canyons

Populus-Salix stream-side association

Typically developed in less exposed situations than preceding, as bottoms of V-shaped ravines and moist shaded slopes

Canyon forest association

Typically developed in moist ravines or slopes with humus soil; or, in the higher foothills, in moist patches of the granite-gravel upland

Aspen association

Dominant plants shrubs, or rarely reaching tree size
Plants larger, comparatively well separated; plant composition variable; ranging also into xerophytic habitats
Foothills mixed shrub association
Plants smaller, low, closely set, usually in fine moist soil
Symphoricarpos association
Dominant plants herbaceous. . . . *Foothills mesophytic grassland association*

Descriptions of associations

The plant communities are described in the order of their appearance in the foregoing synopsis. They are subject to greater geographic variation than can be treated fully in this article; mention is made, however, of the more considerable variations. The space allotment is not always proportionate to the importance or general interest attaching to the several associations; some are already fairly well known, some are less variable or can be summed up more concisely than others, and some have been less thoroughly or less widely studied. An approach to a balanced treatment has been sought by the use of a smaller type for statements of less general significance, descriptions of minor or very local vegetation divisions, and detailed passages included by way of illustration or amplification.

Plant names, when appearing without citation of authorities, may be understood to be as in COULTER and NELSON'S *Manual* (**2**), which in general follows the usage recommended by the Vienna Congress. The unit of vegetation is the plant association, in the generally accepted sense; its distinctive representations, appearances, or variants are spoken of as consocies; the terms as used are described in an earlier article (**24**, p. 382, footnote). Index letters attached to species names signify frequency or abundance or regularity of occurrence, as follows: *a*, abundant; *f*, frequent; *i*, infrequent; *l*, local or locally; *ch*, characteristic in the community or situation mentioned.

It will be understood that the total number of species of plants occurring in an area so extensive as that of this study is very large. No attempt has been made to work out the complete floristics, or the floristic variation of the several communities as represented in different localities. Field botanists will remember that very many of the species making up the flora of a region are rare, known from a single or very few stations, are in effect of very slight ecological significance, so far as vegetation is concerned. A further considerable proportion is not found in extensive plant assemblages (as, in this study, grass species occurring only in stream margins), and is not important as part

of the vegetation of the general area. Several or numerous species of certain genera, again, may be of similar habitat distribution, so that a species of one locality may be replaced in the same habitat in another locality by a second species of that genus. Care has been taken to select species for the floristic lists which are as representative over a considerable area as may be. In the southern foothills, as in the plains of southern Colorado, many more plants of southwestern derivation enter into the flora, particularly in the primitive grassland and mixed grassland assemblages. Many are true desert plants; a few cacti and chenopods and many composites fall in this group. That this geographic variation from north to south is ecological as well as floristic should be apparent. It is paralleled by a similar altitudinal variation in composition, from the montane zone to the plains.

LICHEN ASSOCIATIONS

TUCKERMAN (**23**); WILLIAMS (**27**), lichens in the Black Hills; HERRE (**7**), lichens of Mount Rose, Nevada; SHANTZ (**22**, p. 187).—Fig. 2.

A considerable proportion of the area of the foothills is exposed rock, and its vegetation, except in crevices, is mostly composed of lichens. The study of lichen vegetation has usually been left to the specialists in that group of plants, since they are so poorly known to most other botanists. For this reason brief notes on external appearance, as to color and vegetative form, are given with the species names. The writer is indebted to R. HEBER HOWE, Jr.,[2] who has made the species determinations and examined this part of the manuscript (fig. 2).

Dry surfaces, much exposed to sun and wind, occupy most of the area of bare rock in the foothills. They slope considerably, so that run-off is rapid and absorption minimal. The first lichens to invade dry rock, forming primitive xerophytic stages of lichen growth, are fine-grained crustose forms, notably the black-gray *Rinodina radiata* Tuck. (?=*R. thysanota* Tuck.) and an indeterminable lead-gray species which is especially characteristic. These are soon followed, but not displaced, by lichens of an intermediate stage, mostly coarser crustose forms; the gray-green *Rinodina oreina* (Ach.) Wain. is a character species both locally and geographically abundant. The established stage on dry rock is marked by the gray-green small-foliose *Lecanora rubina* (Vill.) Wain. and the

[2] Some of the crustose species were determined for Dr. HOWE by H. E. HASSE; the *Stereocaulon* by L. W. RIDDLE.

larger-foliose, also gray-green, *Parmelia conspersa* (Ehrh.) Ach., which may be said to be the dominant and most frequent lichen of exposed rock. Here also occur the gray-green crustose-foliose *Rhizocarpon geographicum* (L.) DC., with *Rinodina oreina* persisting from the preceding stage, and a few other species, including one or two of *Parmelia*, *Gyrophora erosa*, and the large and peculiar *Gyrophora vellea* (L.) Ach., in crisped-margined dirty-gray plates 0.25–2 inches in diameter, attached centrally beneath. These

FIG. 2.—Lichens on steep rock-wall of rather sheltered side-canyon opening northward into Boulder canyon; dark masses at joints are cushions of *Selaginella*.

established stages appear to be self-perpetuating so long as physical conditions of dry rock are unchanged.

Less exposed, but usually dry, surfaces, such as shaded rocks, overhangs, surfaces dripping for some time after rains, recesses in joints, etc., have also characteristic lichen assemblages and definite successions. The earlier lichens include the yellow-green crustose *Acarospora xanthophana* (Nyl.) Fink (characteristic and abundant), with *Lecanora rubina*, *Rhizocarpon geographicum*, and *Rinodina radiata*. *Acarospora* persists in the established stages, which also show the bright orange-brown crustose-foliose *Caloplaca elegans* (Link.) Th. Fr. (characteristic and abundant), *Parmelia conspersa*, *P. sulcata* Tayl., *P. conspersa* var. *stenophylla*? Ach., *Gyrophora vellea*, and other species. Considerably less of the rock surface remains uncovered with lichens here than in the xerophytic situations, and the number of species is larger, although the area of this

habitat and its lichen assemblage is very much smaller. *Caloplaca elegans* and *Parmelia sulcata* are frequent on scattered rocks and tree trunks in shaded canyon-bottoms.

Moist surfaces in humid recesses of the rocks show numerous lichen species, mostly foliose, including *Physcia aipolia* (Ach.) Nyl. and a number of species of *Parmelia*. Mosses grow with the lichens abundantly in these situations. These distinctly humid recesses are scattered and infrequent in the foothill region. A *Cladonia*, probably *C. fimbriata* (L.) Fr., is characteristic on moist north-facing canyon slopes, amongst mesophytic herbs, or beside surface rocks. A pulvinate, finely divided whitish fruticose lichen, *Stereocaulon albicans* Th. Fr., has the growth-form of a pulvinate moss, being "rooted" in moist rock crevices, although the aerial part is more or less exposed. It is infrequent.

SUMAC ASSOCIATION

ROBBINS (**16**, p. 46), distribution on Long Mesa near Boulder.

As indicated in the synopsis of associations, the shrubs of sumac (*Rhus cismontana* Greene, which is so like *R. glabra* of the eastern states as to be considered identical with it by some botanists) often form a new plant assemblage in denuded xerophytic situations. These are extremely variable, including old roadways, rock talus below road embankments, quarries, or prospect holes, stony hillsides where erosion or landslipping has removed much of the plant cover, or places which have been burned. In the lower foothills, and at the mountain-front, the sumac appears to be quite common after fires, the slopes being too dry to allow the establishment of aspens, in most places. The shrubs are usually separated, the sparse plant cover of the interspaces often being composed of plants of the primitive grassland association. As developed in the foothills, the assemblage shows no essential difference from the sumac growths of many parts of the United States. In autumn the bright red coloring of the leaves makes the community very conspicuous, so much so as to give an exaggerated notion of its frequence of distribution.

FOOTHILLS PRIMITIVE GRASSLAND ASSOCIATION

CLEMENTS (**1**, pp. 9–12), gravel slide formation, half gravel slide formation, in part; RAMALEY (**12**, pp. 124–128), *Cercocarpus* scrub, upland dry grass, and foothill sagebrush-grass formations, in part; SCHNEIDER (**21**), gravel slide and half gravel slide formations, in part.

The principal herbaceous growth of dry coarse-soil situations in the foothills presents very great variability, and is very generally distributed, occupying not only large areas by itself, but occurring in mixture with shrubs and trees representing different associations. It is perhaps not too much to say that only a small proportion of

the area in which the rock pine is of frequent occurrence is occupied by actual forest; the usual vegetation of the pine-sprinkled upland is open, the ground-cover is made up of associations of herbaceous plants or low shrubs; prominent among these is the primitive grassland. It enters largely into the ground-cover of other mixed associations also, in which trees and shrubs other than rock pine are conspicuous. The variability of such an open ground-cover as the primitive grassland is so great that no particular set of plants can be said to characterize the whole community, although certain features are common to all of its variants or consocies: (1) they constitute the first vegetation in new and unfavorable habitats; (2) this vegetation is sparse and open; (3) it is made up of an assemblage of species typical of coarse soils and rather considerable exposure to sun and wind, some more commonly in the plains, others in the mountain region (many of these plants are common to several of the consocies, though some few are typical only in the more extreme developments of particular consocies-habitats, as *Erigeron compositus* in packed granite-gravel); (4) as development of vegetation proceeds in the several consocies, with accumulation of the plant remains, closing of the plant cover, etc., they resemble one another more closely, converging into a less open growth, which may be known as the foothills dry grassland association, the next higher in the genetic series. Many of the species of the primitive grassland seem not to be particularly xerophytic, as *Thlaspi coloradense* and *Gilia aggregata*, for these are active during the early part of the season, when the moisture supply is ample. Such plants are very widely distributed in the foothills and are not characteristic of particular habitats nor of the species groupings of particular plant communities.

A partial list of species of the primitive grassland follows:

SPECIES LIST: PRIMITIVE GRASSLAND

Selaginella densa (*l*)	Phlox multiflora
Aristida longiseta (*l*)	Gilia aggregata
Stipa comata (*l*)	Gilia pinnatifida
Bouteloua hirsuta (*l*)	Phacelia heterophylla (*ch*)
Koeleria cristata (*ch*)	Oreocarya virgata
Sitanion brevifolium (*l*)	Pentstemon humilis

Arenaria Fendleri
Paronychia Jamesii (*ch*)
Berberis aquifolium
Thlaspi coloradense
Physaria floribunda (*l*)
Lesquerella montana
Sedum stenopetalum (*ch*)
Potentilla pennsylvanica strigosa
Potentilla Hippiana
Astragalus Purshii
Geranium Parryi (*ch*)
Mentzelia spp.
Chrysopsis villosa (*ch*)
Chrysopsis spp. (*ch*)
Townsendia exscapa
Townsendia grandiflora
Machaeranthera aspera
Helianthus pumilus
Hymenoxys floribunda (south)
Gaillardia aristata
Artemisia frigida (*ch*)
Artemisia gnaphalodes var. (*ch*)[3]
Senecio Nelsonii (*ch*)

The more important representations of the association in special habitats:

(1) The mixed consocies of mixed detrital slopes. This term may be applied to the very sparse plant community of slopes on which the fragments of rock-débris are of all sizes, and in which as a result conditions for plant life vary extremely locally. The vegetation may be regarded as a mosaic of different variants of primitive grassland, with the addition of certain components from other vegetation types, as the lichen, shrub, and pine associations (see figs. 4, 8).

(2) The *Geranium-Chrysopsis* consocies of unstable granite-gravel slopes, in which the loose bunches of these two plants are the most frequent or the only plants in the loose decomposed granite soil.

(3) The *Artemisia frigida-Koeleria* consocies of stony detrital slopes (rock talus, frequently). The habitat is quite common though seldom very extensive; the sage may be very abundant without the grass *Koeleria;* it is an important species in the northern Great Plains and in the mountains up to 10,000 ft.

(4) The compacted granite-gravel consocies. Dwarfed plants of *Erigeron compositus*, *Senecio Nelsonii*, and a few other species are characteristic in level or gently rolling top surfaces, on which the thin coarse soil has become compacted into a hard floor (fig. 3). In its most extreme condition seen, the *Erigeron* was the only plant, occupying less than 4 per cent of surface. Rather infrequently, *Potentilla Hippiana* occupies these situations, forming a pure growth which spreads vegetatively.

(5) The mat consocies of gravel slides. These habitats are more frequent in the Pike's Peak highland than in the Front Range proper, where they are

[3] This plant has narrow pinnately 5-divided leaves, and appears to be quite constantly different from the entire or apically 3-divided form with dense white canescence. With this structural difference is an apparently constant habitat difference; the dissected form is usually in very coarse soil, the other in clay, abundant only at the mountain-front. It is hoped that experiments can be made on these to determine whether the forms are genetically distinct, as they are ecologically.

best developed on south-facing slopes, commonly at the bottoms of open canyons, beside graded roadways. Species of *Gilia*, *Physaria*, *Phacelia*, *Berberis*, *Gaillardia*, and *Pachylophus* are characteristic. Gravel slides have been studied by CLEMENTS, and by SCHNEIDER (**21**).

The primitive grassland is closely related to certain associations of the Plains region, notably the mat association (**9,** p. 376; **24,** p. 393), and the *Gutierrezia-Artemisia* association (**24,** p. 398), and to the other primitive assemblages leading to short-grass. It is more generally distributed, as would be expected, at lower elevations

FIG. 3.—Granite-gravel floor, with much bare surface, some primitive grassland, and mats of *Arctostaphylos;* in background rocky summit or knob, with scattered pines; Flagstaff Mountain.

and more southerly parts of the mountain region, and in the more exposed habitats. It probably occupies a larger proportion of the total area in the lower parts of the Front Range than any of the other associations in their unmixed condition.

ROCK PINE ASSOCIATION

CLEMENTS (**1**); RAMALEY (**10, 12, 14**); ROBBINS and DODDS (**18**), distribution of conifers on the mesas near Boulder; SHANTZ (**22,** p. 184); WATSON (**25,** p. 207); YOUNG (**28,** p. 337).

Pinus scopulorum, variously called the rock, western yellow, or bull pine, is the important tree in the foothills. Its plasticity

is remarkable, growing in all kinds of soil, on slopes of every angle and every direction, through wide variations in soil moisture, evaporation, light, and temperature. Its wide geographic and altitudinal range is an expression of this plasticity. In favorable situations it grows rapidly, with straight trunk and branches regularly arranged; in the more exposed places it is reduced in size, and commonly gnarled and irregular. Distribution of the pines is largely a matter of establishment, since the critical stages are seed burial, germination, and the young seedling period. Crevices and soil-filled spaces between rocks, usually of small area, afford lodging places for the seeds; exposed summits and slopes of fine soil are mostly covered with grassland. Small areas of soil deposition may allow burial of many seeds, and consequent development of dense young stands. Seeds germinate well in the tangled mats of *Ceanothus Fendleri* (see under *Ceanothus* association). The first few years of the seedling are safely passed only when several favorable seasons are successive (at least in exposed situations), as shown by RAMALEY (**13**, p. 30) for the high mesas near Boulder.

According as establishment is abundant or very sparse in a given station, the growth is closed, giving a true pine forest, or scattered, resulting in the well known open or parklike appearance; this is a mixed vegetation of which the pines form only one component. They may later dominate the whole area if new pines can germinate beneath, but on the whole the closed pine forest is relatively infrequent. Just how important an influence in the foothills fire has been, and is, is very difficult to determine; it is said by some residents that the whole region just north of Boulder Creek was once much more extensively forested than now; but if fire is of fairly frequent occurrence in a region, it is an environmental factor to be taken into account. Its effect is wholly favorable to the grasslands and primitive growths, at the expense of the pines (fig. 4).

In the lower and more southerly parts of the foothills, dry grassland and particularly primitive grassland form the ground cover in most areas of scattered pines. The spiny shrub *Ceanothus Fendleri* is also commonly seen between the trees. Away from the individual trees, and often even at their very bases, the plant cover is mostly not different from its condition where

there are no pines. The trees frequently do modify conditions of growth for ground plants, however, where pine needles accumulate, but this effect is very local. Farther up, and to the north, and apparently more closely associated with pine growths, the bearberry (see under *Arctostaphylos* association) is an important part of the ground-cover between scattered trees.

Juniperus scopulorum is an infrequent though locally conspicuous tree species found with the pines. *Pseudotsuga mucronata* also mixes in to some extent, even in a few fairly xerophytic stations. *Juniperus communis sibirica* is a ground shrub of infrequent occurrence. *Pinus flexilis* is very locally represented, although not confined to the foothills. *Pinus Murrayana*, the

FIG. 4.—Shallow ravine head; mostly grassland, with fine soil at bottom, and thinner and rockier soil on side-slopes; in coarse soil are numerous pines and *Arctostaphylos* (foreground); in middle ground a considerable clump of *Prunus demissa* (leafless condition), occupying soil moist from seepage; April 1914.

lodgepole pine, of the montane zone, mixes with the rock pine in the upper foothills. The rock pine is by no means absent from the montane zone, and is even quite abundant there if the lodgepole is absent, as in the Pike's Peak highland generally.

The pine association in its unmixed form (practically closed forest) has very few open spaces. Natural pruning of the lower branches is general. Old needles strew the ground; the light is much reduced; the two influences, mulch and shade, acting together or singly, exclude practically all ground plants from the closest stands, and all but a few from less dense forests. Plants of primitive grassland very seldom persist in shade. Relics of former vegetation are seen in less advanced stages, including occasional plants of *Opuntia*, *Cercocarpus*,

bunch-grasses, and others. A few species commonly found in the undergrowth of unmixed but not densely shaded forest are *Harbouria trachypleura*, *Aletes acaulis*, *Senecio* (one or two spp.), *Solidago* (several spp.), and *Pentstemon humilis*.

PINYON-CEDAR ASSOCIATION

CLEMENTS (**1**, p. 8), foothill woodland formation; SHANTZ (**22**, p. 184); WATSON (**25**, pp. 205–207), cedar and pinyon formations.

The pinyon, or nut pine, *Pinus edulis*, and less abundantly the cedar of the southern Rockies, *Juniperus monosperma*, are conspicuous plants in the mountain-front of the southern part of the state and in the adjoining foothills. Toward the south conditions are generally more xerophytic at the mountain-front; there the rock pines are common only in higher elevations; they are replaced below by the pinyon. Like the rock pines farther north, the pinyons show local extension eastward into the plains, in rocky habitats, such as the canyon-walls of rock outcrops, and the bluff-crests of the plains stream valleys.

Between the trees are plains or semi-desert plants, many southerly species being present which are rare or absent farther north than about Colorado Springs. One of the most notable of these is the candlestick cactus, *Opuntia arborescens*, common at the mountain-front on rock-strewn slopes and mesas.

The pinyons (and to a smaller extent the cedars) are typically broadly rounded, the diameter of the crown being usually as great as the height of the tree, which is rarely more than 12–15 ft. The trees are usually separated so that the crowns are distant from each other by a diameter or a little less, in the closer stands. The writer has never seen a really closed pinyon forest in which the crowns would form a continuous canopy. The interval between trees increases with xerophytism and exposure, and the branches are less symmetrically developed. Where the habitat is extensive, the pinyons are quite uniformly dotted over the general area. On rocky ridges and mesa-crests the trees are in ragged lines, in small clumps, or irregularly scattered.

QUERCUS ASSOCIATION

CLEMENTS (**1**, p. 6) and SHANTZ (**22**, p. 179), foothill thicket formation, in part; WATSON (**25**, pp. 207–210), white oaks in the yellow pine association.

East of the range-crest oaks may be seen nearly as far north as Denver; however, they form more extensive growths to the southward. North of the Platte-Arkansas divide they are perhaps more abundant at the mountain-front and in the Plum and Cherry Creek

valleys than in the foothills proper; they range into finer soils than do the pines. In the foothills as well as at the mountain-front the oaks may share mixed rocky slopes with local representations of *Cercocarpus*, pinyon, rock pine, or grassland associations, or may alternate with them. The extent to which they replace the rock pine on south-facing foothill slopes is appreciable even north of Perry Park, and is increasingly considerable southward. There is no apparent reason why they would not grow north of their

FIG. 5.—Alternation of mixed grassland and oak forest, west of Castle Rock, July 1913; tall herbs conspicuous at border.

present limits in the mountain-front; some of them extend north on the west side of the range-crest even into Wyoming (fig. 5).

The taxonomic condition of these oaks is one of confusion. RYDBERG'S *Flora of Colorado* (**19**) lists 11 species, all occurring at or near the eastern mountain-front. *Quercus Fendleri* appears to be distinct, much more xerophytic, more southerly in distribution. The intergradations with most of the others are such that specific determinations are very difficult. CLEMENTS mentions *Quercus Gunnisonii* as the chief species of the Manitou vicinity. Certain Colorado botanists now speak of the doubtful oaks collectively, for the present, simply as *Quercus* spp. The writer has thus far not been able to distinguish different habitat groups within these *Quercus* spp. (cf. SHANTZ, **22**, p. 179).

So many of the oaks do not reach tree size that the assemblage in many places presents the appearance of chaparral. As might be expected from their wide range of habitat-tolerance, they vary considerably in appearance, from shrubby scattered trees or stunted thickets, to low forest with mesophytic undergrowth. In very favorable stations, as along streams in the southern foothills, the oaks may reach a height of 20 ft. and more. The undergrowth in ungrazed parts of the oak scrub has a decidedly mesophytic stamp during the moister part of the season; *Pulsatilla*, *Castilleja*, *Monarda*, *Calochortus*, *Lupinus*, *Geranium*, *Galium boreale*, *Campanula*, *Thermopsis*, *Danthonia*, *Pentstemon unilateralis*, are typical of oak borders and less densely shaded parts within. Dense closed shaded oak scrub shows abundance of a tall white-flowered umbellifer, *Ligusticum Porteri* (?).[4] Late summer shows many of the less xerophytic composites, including species of *Aster*, *Solidago*, *Erigeron*, and *Brickellia grandiflora* var. *minor*. The undisturbed clumps of small oak trees, where these alternate with dry grassland, are often bordered with tall, rather mesophytic herbs, as *Lupinus argenteus*, *Monarda* spp., and *Achillea millefolium* L. (*A. lanulosa* Nutt.), as may be seen in fig. 5, taken west of Castle Rock.

Low scrubby oak thickets, in grazed areas, are mostly impenetrable to horses and cattle; they are, however, eaten from the outside, and the patches thus slowly reduced in area. This results in a complete replacement of oak by grassland, as stated by SHANTZ (**22**, pp. 182, 203). When, however, the height of the small trunks in the middle of a clump becomes too great for the animals to reach the top leaves, their safety is assured. In these taller growths the lower parts of the trees are much less dense; if there is no outer border of dense thicket, grazing animals are enabled to enter; the assemblage is now a scrubby forest of low trees, with open spaces between the trunks and very scanty undergrowth, as in fig. 6. Grazing animals may thus have a large part in determining the character and distribution of the oak vegetation.

CERCOCARPUS ASSOCIATION

CLEMENTS (**1**, p. 6) and SHANTZ (**22**, p. 179), foothill thicket formation, in part; RAMALEY (**12**, pp. 124–126), *Cercocarpus* shrub formation; RAMALEY and ROBBINS (**15**), local distribution in a square mile of rock ridge and foothills; SCHNEIDER (**21**, p. 292), thicket of south slopes, in part.

Ragged shrubs of *Cercocarpus parvifolius*, or, as it is called, mountain mahogany, form a characteristic vegetation in dry exposed rocky places, particularly along the mountain-front, on butte-slopes, hogback ridges, stony mesa-crests; in the foothills it is most abundant on south-facing side-slopes, or on the outermost slopes facing eastward on the plains. The stony fragments of the

[4] Either *L. Porteri* C. and R., or *L. affine* A. Nels., as determined by E. E. SHERFF.

soil vary from those of coarse granite-gravel to the variously sized blocks of rock talus.

The shrubs are 2–5 ft. high, very loose in habit, with few branches and reduced leaf surface. The fruits are provided with long plumed awns. The plants are separated, being regularly spaced like the pinyons, the intervals likewise varying with degree of exposure. The habitat relations of *Cercocarpus* are in fact quite like those of the pinyon, and it is north of the pinyon area that the mountain mahogany association is best developed. The interspaces

FIG. 6.—Open grove aspect of oak assemblage, caused by entrance of grazing animals, Perry Park; open mixed grassland in coarse soil occupies foreground.

between plants may be almost bare, or may be occupied by a sparse growth of xerophytes, most of them plains plants or representatives of the primitive grassland, the mat growth-form being common.

ARCTOSTAPHYLOS ASSOCIATION

COWLES (**3**, p. 367) and GATES (**6**, p. 306), Lake Michigan dunes; WHITFORD (**26**, p. 298), northern Michigan. In the Colorado foothills: ROBBINS (**16**, p. 44); SCHNEIDER (**21**, p. 299); SHANTZ (**22**, p. 186).

The *Arctostaphylos-Juniperus* association of the northeastern coniferous forest region is very well known to students of vegetation. Practically the same community is represented in the Rocky Mountains, associated there as elsewhere with coniferous vegetation. The same plant species and the same creeping habit are seen. The

important difference, as seen in the Front Range foothills, is that the juniper is very infrequently seen, the *Arctostaphylos* mostly dominating alone.

Conditions of soil-moisture, soil-texture, position, slope, and exposure are varied. The creeping mats of bearberry are seen on rock, in gravelly decomposed granite, and in fine moist humous soil; on practically all slopes, shaded and sunny, and through a considerable range in altitude. The growth is more extensive and more frequent, however, away from the mountain-front, at elevations 800–1200 ft. above the lower limit of rock pine, being increasingly abundant from that height upward, and being perhaps more typical of montane than of foothills vegetation. Its most frequent habitat in the foothills is the rolling floor of the granitic upland, the soil of which is thin, coarse, mostly compacted (granite-gravel). Here the conspicuous vegetation is rock pine, in open array of scattered clumps and single trees. Parts of the treeless surface are occupied by large mats of *Arctostaphylos*, with admixture of *Ceanothus Fendleri* (less of this upward); the rest of the area is bare or nearly so, with a few scattered herbaceous plants, mostly of primitive grassland.

CEANOTHUS ASSOCIATION

ROBBINS (**16**, p. 41); WATSON (**25**, p. 207).

The spiny shrub, *Ceanothus Fendleri*, is ecologically similar to *Arctostaphylos* in many respects. It forms a low, matlike, spreading ground cover, and occurs to some extent in mixture with bearberry mats. It differs from the other in being typical of more exposed and xerophytic slopes, in being abundant at lower altitudes, and more southerly in geographic distribution. MILLARD S. MARKLE informs the writer that the *Ceanothus* community is important in the Sandia Mountains of New Mexico, occurring frequently with the oaks and with *Robinia neo-mexicana*. *Ceanothus* ranges into dry fine-soiled habitats more frequently than *Arctostaphylos*, and is closely associated with grassland, rather than pine forest. It is not evergreen.

Ceanothus shrubs occur in closely set or scattered patches, mostly in unstable gravelly or finer soil of detrital slopes. They have a strongly accelerative part in vegetation-development. Their numerous twigs and thorns, even in the leafless winter condition, catch and hold wind-blown and washed-down soil particles and bits of plant débris, thus stabilizing and adding to the soil, and accumulating humus. In one station this had even resulted in the building of small dunes of wind-blown dust, of about 8 inches height and 18 inches diameter. Seed burial is favored in these mats, as well as germination. Some of the more mesophytic of the foothills plants are seen growing up through the tangled branches; pine seedlings also germinate in the shelter of *Ceanothus*, which may thus be an important factor in reforestation. On dry, burnt slopes *Ceanothus* frequently covers a considerable proportion of surface and, with the *Rhus cismontana* shrub growth, is an important stage in succession after burns.

Ceanothus mollissimus and what appears to be *Ceanothus subsericeus* Rydb. occasionally occur with the spiny species, in the less xerophytic stations. *Ceanothus velutinus* is rare in the lower foothills, but is frequent at higher elevations and farther north. Herbs of the primitive grassland and mixed grassland commonly grow out from between the twigs of *Ceanothus Fendleri*, and to some extent are seen in the spaces between the mats.

FOOTHILLS MIXED GRASSLAND ASSOCIATION

CLEMENTS (**1**), ground-cover in the foothill thicket and pine formations, in part; RAMALEY (**12**), foothill sagebrush-grass formation; SCHNEIDER (**21**), half gravel slide formation, and grassland of north slopes; SHANTZ (**22**), *Bouteloua* formation, in part: its modified form at the mountain-front; VESTAL (**24**, p. 386), *Bouteloua* mixed consocies, as developed at the mountain-front; WATSON (**25**, pp. 209, 210), herbaceous ground-cover in the yellow pine association, and mountain "meadows."

The mixed grassland association normally develops from primitive grassland, one of its important features being the establishment of the dominant *Bouteloua oligostachya*, the grama grass of the plains. It thus differs from the primitive grassland in that (1) the ground cover is less open, though still generally xerophytic; (2) the soil is usually more stable (in most situations a physical cause, rather than the effect, of the more permanent vegetation); (3) the soil is more finely broken up, and to it may be added considerable humus; and (4) a number of plains, prairie, and foothill species absent or rare in the primitive grassland are established.

The assemblage is most heterogeneous, since the many plants include widely diverse ecological, geographic, and floristic types. Extreme xerophytes and relatively mesophytic plants, plants of widely varying growth-form and seasonal relations, of great difference in plasticity to environmental variation, in altitudinal and habitat range, may occur in the same small grassland area. This mixed vegetation is really very closely allied to the modified plains grassland mentioned as the *Bouteloua* mixed consocies of the short-grass association (**24**, p. 386). This is found in the mixed mesa soils of the mountain-front zone just outside the foothills. The conditions which would result in heterogeneity of the grassland vegetation are probably similar in the lower foothills to those of the mountain-front; some of these are given in the article cited (**24**, pp. 381, 382).

So many species occur regularly in the mixed grassland, and the variability in floristic composition in particular stations is so great, that a selected list of plants equally representative of various localities and habitats cannot be

given. By way of illustration, however, a list of the plants observed in a particular mixed grassland station may be presented, and this is followed by a list of some other species commonly found in the community, but which happen to have been absent from the station selected. The station is on the east slope, not far from the top, of a hill a little over two miles west of the mountain-front and a little north of Boulder, in section 36, T 2 N, R 72 W. The hill is marked in the Boulder quadrangle of the United States topographic atlas by the altitude of its summit, 7168 ft. The spot studied most in detail is at about 7000 ft.; exposure is considerable, as the slope is even and treeless; drainage is probably quite rapid; the soil coarse, with but little humus; proportion of bare surface about 15 per cent on June 18, when the list was made. All of the plants marked as abundant or frequent occur in practically every square meter of surface.

PLANT COMPOSITION OF A TYPICAL MIXED GRASSLAND STATION

Bouteloua oligostachya (*a*)	Eriogonum umbellatum (*i*)
Phacelia heterophylla (*a*)	Opuntia polyacantha (*i*)
Chrysopsis villosa (?) (*a*)	Oreocarya virgata (*i*)
Senecio oblanceolatus (*a*)	Artemisia gnaphalodes var. (*i*)
Geranium Parryi (*a*)	Astragalus flexuosus (*i*)
Artemisia frigida (*a*)	Eriocoma cuspidata (*i*)
Aragallus Lambertii (*a*)	Mamillaria vivipara (*i*)
Koeleria cristata (*f*)	Sitanion brevifolium (*i*)
Lesquerella montana (*f*)	Gaillardia aristata (*i*)
Mertensia lanceolata (*f*)	Phlox multiflora (*i*)
Linum Lewisii (*f*)	Potentilla pennsylvanica strigosa (*i*)
Carex pennsylvanica (*f*)	Euphorbia robusta (*i*)
Gilia pinnatifida (*lf*)	Aletes acaulis (*i*)
Gilia spicata (*lf*)	Poa longipedunculata (*i*)
Helianthus pumilus (*lf*)	Eriogonum alatum (*i*)
Cerastium arvense (*lf*)	Townsendia exscapa (*i*)
Aragallus albiflorus (*lf*)	Townsendia grandiflora (*i*)
Stipa comata (*lf*)	Allium sp. (*i*)

The order in which the species are listed gives a rough approximation of their relative importance as making up a part of the vegetation, in descending scale. The names of plant species elsewhere frequent in the association follow:

ADDITIONAL SPECIES FREQUENT IN MIXED GRASSLAND

Woodsia oregana	Echinocereus viridiflorus
Selaginella, two spp.	Gaura coccinea
Aristida longiseta	Cymopterus acaulis
Muhlenbergia gracillima	Gilia aggregata et spp.
Poa crocata	Lithospermum multiflorum

Poa Fendleriana	Onosmodium occidentale
Agropyron Smithii	Pentstemon humilis et spp.
Elymus triticoides	Castilleja integra et spp.
Leucocrinum montanum	Campanula rotundifolia
Calochortus Gunnisonii	Liatris punctata
Yucca glauca	Grindelia squarrosa
Zygadenus intermedius	Chrysopsis spp.
Comandra pallida	Solidago spp.
Allionia linearis et spp.	Aster spp.
Pulsatilla hirsutissima	Machaeranthera aspera et spp.
Argemone intermedia	Erigeron spp.
Corydalis aurea	Ratibida columnaris
Draba spp.	Helianthus spp.
Erysimum asperum	Hymenopappus filifolius
Potentilla spp.	Hymenoxys floribunda
Astragalus spp.	Artemisia aromatica
Psoralea tenuiflora	Artemisia canadensis
Malvastrum coccineum	Senecio plattensis et spp.
Viola Nuttallii	Senecio spartioides
Mentzelia spp.	Nothocalais cuspidata

As regards distribution of the mixed grassland association in the foothills, it may be said that the primitive grassland is more frequent and occupies areas of greater extent, because of the general instability and rocky character of the sloping surfaces. In the upper foothills mixed grassland is absent from compacted soil level or rolling surfaces generally occupied by pine and *Arctostaphylos*, etc., but dominates on the more exposed mountain sides, which are treeless. The mixed grassland, like primitive grassland, is subject to a gradual ecological and floristic variation, from the south northward, and from the short-grass of the plains to the montane dry grassland of elevations from 8500 to 10,000 ft.

BUNCH-GRASS ASSOCIATION

CLEMENTS (**1**, p. 6), *Andropogon*, etc.; SCHNEIDER (**21**), half gravel slide formation, in part; SHANTZ (**22**, p. 43), *Bouteloua hirsuta* consocies, with *Andropogon* spp., *Atheropogon*, etc.; VESTAL (**24**, pp. 388–390), bunch-grass association: photograph and citation to descriptions in other regions; WATSON (**25**, p. 209), *Andropogon*, etc.

The bunch-grass vegetation of the foothills is quite similar to that of the mountain-front and over the whole prairie region, including most of the same species, but containing in addition other grasses of similar growth-form but of different geographic distribution. With the bunch-grasses are many composites and other

plants of the mixed grassland, such as *Liatris*, *Chrysopsis*, *Eriogonum alatum*, etc. The tufted bunch-grass growth-form is well known; the roots are deep and numerous; the plants are mostly late in flowering; they are active during the whole growing season, depending on a constant moisture supply. The chief habitats in the foothills which satisfy this condition are rocky or very coarse gravelly slopes, exposed and dry at the surface, but with rather more moisture beneath than in most areas of mixed grassland; these situations are consequently rather locally developed only.

PRAIRIE BUNCH-GRASSES OCCURRING IN FOOTHILLS

Andropogon scoparius (*a*)	Muhlenbergia gracilis (*f*)
Andropogon furcatus (*a*)	Sporobolus heterolepis (*lf*)
Hilaria Jamesii (*li*)	Atheropogon curtipendulus (*f*)
Sorghastrum nutans (*lf*)	Koeleria cristata (*f*)

OTHER FOOTHILLS PLANTS OF BUNCH-GRASS TYPE

Trisetum montanum (*l*)	Agropyron spicatum
Festuca confinis (*l*)	Sitanion longifolium
Agropyron occidentale (*l*)	(?)Elymus triticoides

Hilaria is a southern plant and has not been seen north of about Canyon City. *Sorghastrum* and *Hilaria* appear not to extend far into the foothills. *Koeleria* ranges into many widely varying habitats and is found with many different plant assemblages. This may partly be due to its early ripening (it flowers in June), which may allow it to escape the dryness of the latter part of the season. Most of the plants of the second group bloom in early summer also; they are frequently found in clumps of one species, in rock crevices or coarse soils. *Trisetum* ranges into the montane zone, but not into the plains; it is restricted to moister places than most of the others. *Agropyron spicatum* is one of the chief dominants of the extensive grassland areas in the northwestern states, in intermontane valleys and the Columbia Basin plains. It too matures early in summer and is dried up the rest of the season. *Elymus triticoides* is included with some hesitation; it may be more like the grasses of the primitive bunch-grass type (**24**, p. 397).

PSEUDOTSUGA ASSOCIATION

CLEMENTS (**1**, p. 14); SCHNEIDER (**21**, pp. 299, 300), with list of herbaceous plants; RAMALEY (**14**, pp. 251, 262); WATSON (**25**, p. 211); YOUNG (**28**, p. 343).

The Douglas "spruce," *Pseudotsuga mucronata*, is, like the rock pine, one of the most abundant and widely distributed conifers of

western North America, but in the foothills of the Front Range in Colorado it is relatively very local in occurrence. It is frequent only on north-facing slopes and in canyons, where the snow lies deep and late. It grows in close stands or as scattered trees (fig. 7).

Small trees of *Juniperus scopulorum* may occur infrequently in the *Pseudotsuga* forest; in unshaded areas with moist soil a few aspens may be found. *Arctostaphylos* and the prostrate *Juniperus communis sibirica*, so frequently associated with it, are seen as relics. The moist and sheltered slopes on which *Pseudotsuga* grows may in its stead be covered by the mesophytic grassland association, and many of its plants occur scattered among the conifers, such as

FIGS. 7, 8.—Fig. 7, *Pseudotsuga* association on a north slope; fig. 8, another general view, showing prevalence of grassland on side-slopes; trees conspicuous in profiles of distant slopes.

Mertensia spp., *Campanula rotundifolia*, *Pulsatilla hirsutissima*, *Saxifraga rhomboidea*, *Aster laevis*, and one or two small ferns.

The rock pine grows well in the moist habitats of the *Pseudotsuga*, if the young trees can get a start, and so the two species are commonly found in mixture, especially toward the top of canyon-slopes and in other less protected places. Also *Pseudotsuga* can range into the habitats of the pine, where, however, it is usually of less symmetrically spire-shaped form, and with fewer and uneven branches, so that the growth habit resembles that of the pine.

POPULIS-SALIX STREAM-SIDE ASSOCIATION

RAMALEY (**12**, p. 127, **14**), part of the canyon forest formation; WATSON (**25**, p. 21), *Populus angustifolia* society; YOUNG (**28**, pp. 330–336).

The poplars and willows of stream-sides form a nearly continuous belt in the wider and more open canyon-bottoms of the foothills. *Populus angustifolia*,

the narrow-leaved cottonwood, is the largest and most frequent species. The willows include *Salix irrorata* and *S. exiguus*, forming shrubby clumps; and *S. Bebbiana*, *S. amygdaloides*, and *S. lasiandra*, small trees. The hackberry, *Celtis reticulata*, is perhaps more typically found scattered along stream-sides in quite exposed places than with other trees. It is also common in such habitats in New Mexico. Certain plants common in the canyon forest are also quite characteristic, in the rather less exposed stream-side situations, replacing the cottonwoods and willows in small areas, or intermingling with them. Such plants are *Alnus tenuifolia*, *Betula fontinalis*, *Acer Negundo*, and the shrubby *Cornus stolonifera*. Scattered plants of the mixed shrub association are also frequently seen: *Bossekia*, *Ribes*, *Rosa*, *Crataegus*, *Prunus demissa*, and others.

CANYON FOREST ASSOCIATION

RAMALEY (**12**, p. 127); YOUNG (**28**, pp. 333, 335), *Alnus-Betula-Corylus* assemblage; (*l.c.*, p. 334), *Crataegus* assemblage, etc.; DANIELS (**4**, pp. 21, 27).

The canyon forest, which contains many of the deciduous tree species of the foothills, is typically developed in local mesophytic stations, such as the slopes and bottoms of narrow canyons, in which the soil is moist (usually from seepage), and the air comparatively humid, due to the shade and the shelter from wind. A selected list of species is here given:

PLANTS OF FOOTHILLS CANYON FOREST ASSOCIATION

Trees

Alnus tenuifolia	Prunus americana
Betula fontinalis	Prunus demissa (Nutt.) Dietr.[5] (*ch*)
Salix Bebbiana (*i*)	Robinia neomexicana (*l*)
Populus tremuloides (*li*)	Acer glabrum (*ch*)
Amelanchier alnifolia (*li*)	Acer Negundo (*l*)
Prunus pennsylvanica (*ch*)	Crataegus coloradensis et spp.

Shrubs

Corylus rostrata (*l*)	Rhus Rydbergii (*i*)
Ribes longiflorum	Vitis vulpina (*l*)
Physocarpus Ramaleyi (*i*)	Parthenocissus vitacea (*l*)
Rosa Sayi et spp.	Viburnum pauciflorum (*li*)

[5] JONES (**8**, p. 35) fails "to see any ground for NELSON'S *P. melanocarpa*, even though NUTTALL describes his as red-fruited, for we know that this species has fruit red till dead ripe, when it turns black."

Herbs

Pteridium aquilinum	Fragaria pauciflora et spp.
Smilacina stellata (*ch*)	Aralia nudicaulis
Smilacina amplexicaulis (*ch*)	Viola canadensis Rydbergii (*ch*)
Stellaria Jamesiana	Castilleja miniata et spp.
Thalictrum spp.	Monarda Ramaleyi et spp.
Aquilegia coloradensis	Hydrophyllum Fendleri (*ch*)
Delphinium Nelsonii (*ch*)	Galium boreale (*ch*)
Ligusticum Porteri (?)	Galium aparine
Saxifraga rhomboidea (*ch*)	Galium Vaillantii

The canyon forest presents a wide range of variability, according as favorable ground conditions are uniform or interrupted; thus in rocky canyon-bottoms and slopes it is patchy in development. It may merge into, or mingle with, areas of *Pseudotsuga*, mixed shrub, aspen, *Populus-Salix*, *Quercus*, and moist grassland growths. The herbs especially may be no more typical of unmixed mesophytic deciduous forest than of many other mesophytic habitats. The characteristic plants growing in the shade of large shrubs and trees are *Viola*, *Hydrophyllum*, and one or more species of *Galium*. These are abundant in unmixed canyon forest, at least in the northern foothills.

Amelanchier is an important component only in the upper foothills and the montane zone, or farther north and west in the Rocky Mountains. *Acer glabrum* often occurs by itself on north or shaded slopes, the bushy plants 10–15 ft. in height, and in most places considerably separated. *Prunus demissa*, and several species of *Crataegus* (mostly *C. coloradensis* and *C. cerronis*), together or singly, dominate tall thickets or low forests, which may be regarded as transitional between the mixed shrub and canyon forest associations. In new growths or exposed situations they are low and scrubby; in other places they form a taller and closed growth, with a lower stratum of mesophytic herbs, and may properly be spoken of as forest. *Prunus demissa* and *Crataegus* form relatively much more extensive areas of vegetation in the northern foothills and especially along the northern mountain-front than in the southern part of Colorado. *Robinia* is abundant in the southern third of the foothills area. It ranges into drier habitats, in which it is low and scrubby.

The *Alnus-Betula* consocies has been mentioned as being abundant along mesophytic stream-sides. *Corylus* is frequent only in such situations, occurring in places alone, in others with *Alnus* and *Betula*. The climbers, clematis, Virginia creeper, and grape, are local, and more common in sunny openings. *Viburnum* is in moist canyon-bottoms of the higher foothills.

ASPEN ASSOCIATION

RAMALEY (**14**, p. 251); YOUNG (**28**, p. 347).

Botanists are familiar with the rôle of *Populus tremuloides* in revegetation of burned areas, and it is prominent in the montane zone in Colorado in this capacity. The general area of the lower foothills, however, is too dry for establishment of aspens, and they occur only locally, in ravines even more mesophytic, perhaps, than the ordinary habitat of the canyon forest. Thus in the Boulder area the stations below 7200 ft. in which aspens have been observed in local abundance are very infrequent. Such stations are usually in sheltered ravines with deep humous soil, abundantly moist. The trees in places are large, the undergrowth very mesophytic, with *Thalictrum*, *Heracleum*, *Castilleja* spp., etc., and particularly *Aquilegia coerulea*. At about 7800 ft. in the same vicinity aspens begin to appear in small clumps on the granite-gravel upland, among more frequent clumps of rock pines. No connection with former fires could here be made out; appearances indicated that perhaps there the aspens might be associated with the moist patches resulting from the tardy disappearance of the deeper snowdrifts of winter. The conspicuous yellow color of the aspens in fall probably tends to exaggerate the popular notion of their frequency of occurrence.

MIXED SHRUB ASSOCIATION

DANIELS (**4**, p. 20); RAMALEY (**12**, p. 127), shrubs of the canyon forest; SHANTZ (**22**, p. 179), thicket formation, in part; notes on distribution and ecological relations of the species; RAMALEY (**11**); ROBBINS (**16**); SCHNEIDER (**20**).

The shrub associations of the foothills, like the deciduous tree growths, are generally found in rocky or coarse soil stations with constant moisture supply in the substratum, which is reached by the deep root systems. Local distribution, as in the case of the pines, is probably restricted by unfavorable conditions for germination over a large part of the general area. It has been observed that, on irregular slopes where the distribution of snow in late spring is uneven, the shrubs occupy the moister spots determined by the deeper snow patches. In deep moist soil it is likely that the shrubs are soon succeeded by trees, as has been observed in some stations. The shrub species most commonly found appear in the following selected list. Certain of the canyon forest plants which occur with the shrubs in the less mesophytic stations without attaining tree size are included here also. It is significant that so many of the

shrubs, and some of the canyon forest plants, have fleshy fruits, and so may be distributed by birds.

PLANTS OF FOOTHILLS MIXED SHRUB ASSOCIATION

Ribes saxosum
Ribes pumilum
Ribes vallicola
Ribes longiflorum (*l*)
Jamesia americana (*l*)
Holodiscus dumosus (*l*)
Physocarpus intermedius (*l*)
Physocarpus monogynus (*l*)
Bossekia deliciosa (*f*, *ch*)
Rubus strigosus (*l*)
Rosa Sayi
Rosa arkansana
Rosa Fendleri
Amelanchier alnifolia (*i*)
Crataegus cerronis
Crataegus coloradensis
Prunus americana (*ch*)
Prunus demissa (*ch*)
Robinia neo-mexicana (*l*)
Rhus trilobata (*ch*)
Ceanothus subsericeus

Amelanchier has been mentioned as being rare in the northern foothills, as may be said also for *Holodiscus*. The common shrubs of rock-crevice habitats are *Jamesia* and *Ribes pumilum*. The yellow-flowered *Ribes longiflorum*, unlike the others of the genus, is more frequent in deep, moist, fine-grained soil than in rocky or coarse soil. *Rubus strigosus* is more common in the upper foothills, and in less exposed habitats. It and the roses are smaller than most of the other shrubs. *Prunus americana* forms low dense thickets in rather exposed places. *Robinia* is southern. *Rhus trilobata* ranges into very xerophytic habitats, and can persist and even establish itself on unstable soil of steep or loose slopes. Although a single species may make up the shrub vegetation at any one spot, numbers of them occur together in a very large variety of combinations, particularly where the habitat is internally diverse. The *Cercocarpus*, *Symphoricarpos*, *Ceanothus Fendleri*, sumac, and bearberry associations, on the other hand, show rather constant differences in environmental relations and distribution from the various representations of the mixed shrub association, and consequently have been separated from it. The relation of the mixed shrub association to the canyon forest has already been mentioned; the two grade into each other, but in the main they are quite distinct.

Where the shrubs grow close together, a mesophytic undergrowth of herbs develops. *Galium aparine* or *G. Vaillantii*, *Delphinium Nelsonii*, and *Viola canadensis Rydbergii* are frequent species. The border of many shrub areas, where there is no grazing, shows tall herbs, as *Lupinus*, *Achillea*, *Monarda*, *Pentstemon unilateralis*, etc. Surface rocks, where present in grassland, may allow the scattering admixture of a shrub element, or even, where the soil is sufficiently moist, invasion of shrubs over the general area.

SYMPHORICARPOS ASSOCIATION

RAMALEY (**12**, pp. 127, 128); ROBBINS (**16**, p. 38).

The *Symphoricarpos* association is best developed in moist, fine-grained soil; best seen, in the foothills, on basal or other deep-soiled detrital slopes, clay or loam, with or without humus. The common species of the Colorado foothills is *Symphoricarpos occidentalis*. The bushes are low, are spaced very close together, and are profusely branched, giving the whole growth a very compact and uniformly dense structure, especially where subject to grazing, as in many stations. From its habitat relations, the bush honeysuckle, as it may be called (it is known in some localities as buckbrush), adjoins a semi-mesophytic grassland in most places, competing and alternating sharply with it. Many of the taller mesophytic herbs are seen at the border, including *Frasera speciosa*, *Thermopsis divaricarpa*, the others already mentioned as bordering canyon forest and mixed shrub, and frequently the tall grass *Stipa viridula*. This border condition is best seen where the *Symphoricarpos* assemblage occupies a depression.

The shrub area is dominated by the one species, although bushes of *Rosa arkansana* are mixed in, abundantly in places, and *Berberis aquifolia* may also be seen. A few herbs may occur underneath.

Symphoricarpos in places forms a border between mixed shrub or canyon forest vegetation and grassland.

MESOPHYTIC GRASSLAND ASSOCIATION

RAMALEY (**12**, p. 129), meadow formation.

There are several kinds of herbaceous vegetation in the foothills, of mesophytic or semi-mesophytic character, which may for convenience be considered together. There is a meadow growth, which shades more or less completely into the western prairie-grass of the mountain-front (**24**, p. 390), on the one hand, and into the forest border and forest undergrowth assemblages on the other. On certain shaded ravine slopes a mixture of mesophytic herbs from several of these assemblages has been observed, apparently independent of any tree canopy. The trees affect the herbs, apparently, mainly or wholly by their modification of physical conditions. A selected list of mesophytic and semi-mesophytic species may be given:

MESOPHYTIC AND SEMI-MESOPHYTIC HERBS OF FOOTHILLS

Stipa viridula (*ch*)	Gentiana affinis
Danthonia Parryi (*f*)	Frasera speciosa (*ch*)
Poa pratensis	Mertensia ciliata
Poa Buckleyana	Mertensia lanceolata
Agropyrum violaceum	Monarda menthaefolia (*ch*)

Calochortus Gunnisonii
Zygadenus intermedius (*ch*)
Iris missouriensis (*li*)
Claytonia virginiana
Cerastium arvense (*ch*)
Delphinium Nelsonii (*ch*)
Thlaspi coloradense (*l*)
Erysimum Wheeleri (*ch*)
Saxifraga rhomboidea (*ch*)
Potentilla pennsylvanica strigosa (*ch*)
Thermopsis divaricarpa (*ch*)
Lupinus argenteus et spp.
Lathyrus leucanthus
Viola canadensis Rydbergii
Pentstemon humilis (*la*)
Pentstemon unilateralis
Castilleja linariaefolia (*ch*)
Castilleja sulphurea
Orthocarpus luteus
Galium boreale (*ch*)
Campanula rotundifolia
Aster laevis
Erigeron flagellaris
Achillea millefolium
Arnica cordifolia
Arnica fulgens (*la*)
Senecio integerrimus (*la*)

The prairie grass aspect has already been mentioned, and a description cited. The foothill meadow assemblage in early summer typically shows such conspicuous plants as *Delphinium*, *Cerastium*, *Arnica*, *Senecio*, and *Castilleja linariaefolia* (*C. sulphurea* is frequent only in the higher elevations). The mixed shrub association frequently alternates with meadow, and encroaches upon it, and is bordered by the taller herbs with that assemblage. The forest border and forest undergrowth communities have also been mentioned.

Moist rock crevices in sheltered ravines become overgrown with cushions of *Selaginella* (fig. 2) and smaller cushions of mosses; humus accumulates by the growth and death of these plants; in this *Saxifraga rhomboidea* and later other herbaceous or woody plants may become established. This is a very common successional series from bare rock in mesophytic habitats.

Herbaceous plants commonly seen scattered along the moist soil of stream margins, in open situations, include *Rumex* sp., *Heracleum lanatum*, *Thermopsis*, and *Lupinus*, with certain grasses, as *Muhlenbergia racemosa*, *Eatonia obtusata*, etc.

Hygrophilous and amphibious plants of the canyon streams may for convenience be mentioned at this point. *Marchantia polymorpha* is found on a very few stream margins on rocks or in crevices in sheltered spots. Many mosses may accompany it, especially where some soil accumulates in cracks of stream-side boulders, etc. *Dodecatheon radicatum* may here be found, or species of *Ranunculus* in boggy places. A number of species are seen in these very restricted boggy places. *Mimulus Langsdorfii* and *Veronica americana* may grow there or in quiet little pools of the stream itself. RAMALEY has given these growths the name Stream Bank Marsh Society (**12**, p. 127).

EASTERN ILLINOIS STATE NORMAL SCHOOL
CHARLESTON, ILL.

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VEGETATION OF HAWAIIAN LAVA FLOWS

VAUGHAN MACCAUGHEY

(WITH TWENTY-TWO FIGURES)

Introduction

This paper is a survey of the more important types of vegetation which occur on the lava fields of the Hawaiian Archipelago and their ecological relations. It has particular reference to the spermatophytes, as our taxonomic knowledge of the native land algae, lichens, bryophytes, and pteridophytes is still in a somewhat fragmentary and unsettled condition. The scope of the paper is further restricted by including only the arid or xerophytic districts where the lava flows are relatively barren. Under humid climate the flows rapidly disintegrate into rich volcanic soil and support a luxuriant rain forest. This paper is concerned with the ecology of the xerophytic regions, as these have largely been neglected in the literature of Hawaiian botany.

There is a widespread association of ideas which couples tropical with humid conditions, due no doubt to the many semipopular accounts of the "tropical jungle" and to the types of vegetation usually exhibited in the northern conservatories. It requires a distinct readjustment of perspective to realize that many tropical regions possess large areas of extreme aridity. The Hawaiian Archipelago, situated just within the tropics in the center of the North Pacific Ocean, admirably illustrates this condition. Most of the popular and semitechnical accounts of the islands have emphasized the beautiful humid woodlands and have either ignored or given scant attention to the vast rocky waste lands of barren lava flow and cinder field.

It has been the writer's privilege, during a residence of 8 years in the islands, to have made many expeditions into these arid regions and to have ascended all of the high mountains of the group. This paper is an outgrowth of these trips, some of which have occupied many weeks. In order to make clear the ecological

background of this lava flow vegetation, it is necessary to sketch briefly the salient features of the Hawaiian volcanic mountains. Detailed accounts may be found in such standard works as those of HITCHCOCK, BRIGHAM, DANA, and DUTTON.

It will be noted that the present paper deals largely with the ecological conditions under which the lava flow vegetation exists. A comprehensive annotated list of the lava flow plants is now appearing in the *Journal of The Linnaean Society*.

Classification of islands

From the standpoint of area occupied by lava flows, cinder fields, and other waste lands resultant from volcanic activity, the islands may be divided into two groups: (1) the lesser islands (Niihau, Kauai, Oahu, Molokai, Lanai, Kahoolawe); and (2) the greater islands (Maui and Hawaii, see figs. 1, 2). The lesser islands are, as a whole, of much greater antiquity than Maui and Hawaii. The erosive agencies have been at work for a much longer time, hence the lava flows have been almost wholly turned into soil. There are some traceable flows still existent on some of the lesser islands, Kauai, Oahu (figs. 3, 4, 5), Molokai, and Lanai, for example, but these are relatively non-consequential as compared with the great stretches of lava covered country on Hawaii and Maui. The lava waste lands, *above the timber line*, on Mauna Loa alone, for example, occupy a greater area than the entire island of Oahu, Kauai, or Molokai. Thus a discussion of the vegetation of the Hawaiian lava flows is naturally restricted chiefly to a consideration of the islands of Maui and Hawaii, the largest and youngest end of the long archipelago. No account is given in this paper of the tiny islands which are strewn over a long axis for 1800 miles to the westward of the larger, inhabited islands. Some of these are volcanic rocks, but the majority are tiny reefs and shoals.[1] Their total area is only 6 sq. miles. All are highly xerophytic.

ISLAND OF HAWAII.—Hawaii, the largest island of the archipelago (4015 sq. miles), is about the size of the state of Connecticut, with a maximum diameter of 93 miles (fig. 2). Its area is greater

[1] MACCAUGHEY, V., The little end of Hawaii. Jour. Geography **15**:23–26. 1916.

than that of all the other islands combined. It is composed of 5 volcanic masses. The northernmost, the Kohala Mountains, is of extreme antiquity, deeply eroded, and probably as old as Kauai.

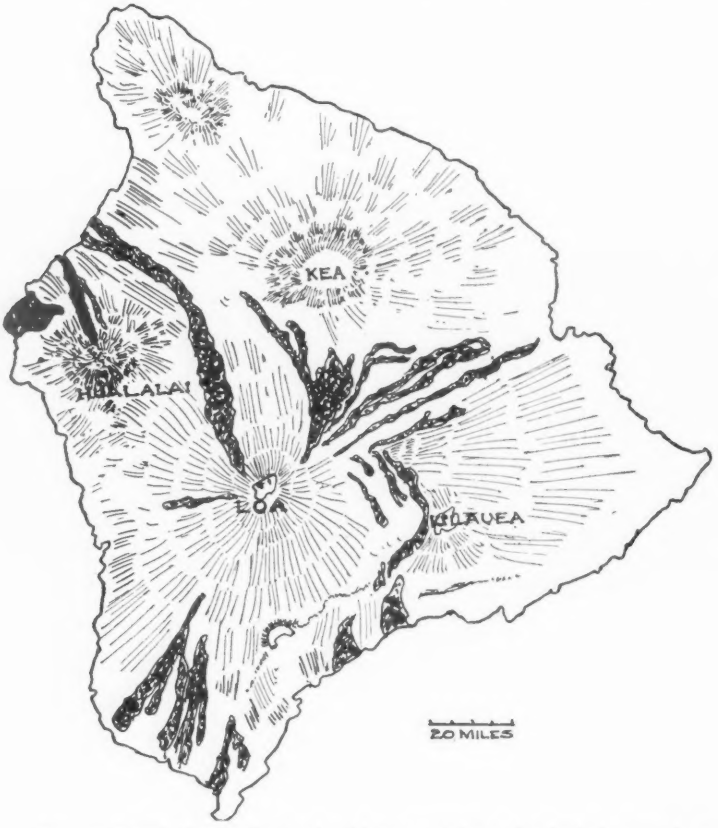

FIG. 1.—Island of Hawaii, showing high mountains and principal recent lava flows.

Mauna Kea and Hualalai, next toward the south, have become "extinct" within comparatively recent times; a lava flow issued from Hualalai in 1801. Mauna Kea has given no manifestations of activity within historic times. It is the highest point within the North Pacific Ocean.

The two southern mountains, Mauna Loa (figs. 6, 7) and Kilauea, are active volcanoes. Their summit craters have exhibited spectacular activity at intermittent periods throughout historic time, and vast lava flows have emanated from their flanks. A large flow issued from the southern slopes of Mauna Loa in May 1916. Loa dominates the island of Hawaii and is the greatest volcanic mountain in the world. The elevations of 5 volcanic

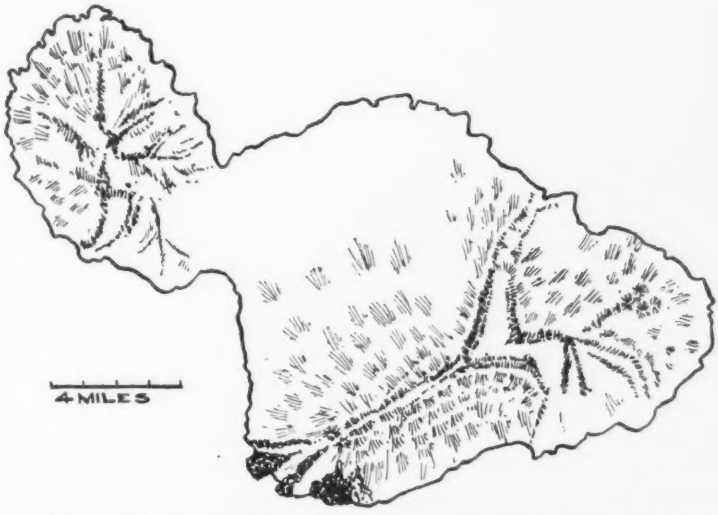

FIG. 2.—Island of Maui: Mount Haleakala comprises entire eastern lobe of island; lava flow country at summit, in caldera, and on southeastern slopes of mountain; regions are largely xerophytic, with exposed lava fields, fields of cinder and ash, cinder cones, and pit craters.

masses of Hawaii are as follows: Kohala Mountains, 5489 ft.; Mauna Kea, 13,825 ft.; Hualalai, 8269 ft.; Mauna Loa, 13,675 ft.; Kilauea, 4000 ft.

HALEAKALA ON MAUI.—Haleakala (fig. 8) is the great mountain that forms the entire eastern portion of the island of Maui. The summit is 10,032 ft. above sea level. It contains a great volcanic caldera, one of the largest in the world, 7.5 miles long by 2.5 miles wide and over 2000 ft. deep. This mountain, often called East Maui, is very much younger than the deeply eroded western mass.

FIG. 3.—Tufa cones and xerophytic lava fields, Oahu; open crater to right, Koko Crater; hill beyond to left, Koko Head.

FIG. 4.—Arid headland, Maka-pu'u, Oahu, illustrating ancient lava sheets exposed by extensive erosion; note stratification of lava flows and erosion of flows at sea level.

Maui is a volcanic doublet made up of two masses of widely different ages. Haleakala probably ceased activity at about the same time as Mauna Kea. The windward, northern face of Haleakala, like that of all the Hawaiian mountains, receives torrential rainfall (400 inches per annum) and is densely covered with jungle forest. The leeward, southeastern slopes are conspicuously arid and barren. In its geological and botanical aspects Haleakala is much more closely related to Kea and Loa on Hawaii

FIG. 5.—Manana or Rabbit Island, deeply eroded tufa cone, isolated as small *barren* islet off windward coast of Oahu, near Maka-pu'u Point; about 2200 ft. long and 400 ft. high, separated from main island by channel of 1 mile; vegetation sparse and stunted, no arborescent vegetation.

than to its associate West Maui. It is separated from Hawaii by a relatively narrow channel, 26 miles wide and 1032 fathoms deep. From the standpoint of this paper it will be considered as one of the Kea, Loa, Hualalai family.

THE FOUR GREAT MOUNTAIN MASSES.—These four great volcanic mountains, Haleakala, Kea, Loa, and Hualalai, closely resemble each other in a number of important ecological particulars: (1) their summits rise 8000–14,000 ft. above sea level and are frequently covered with snow; (2) there is a large treeless zone on the summit of each; this is most extensive on Loa, Kea stands next, then

FIG. 6.—Summit and upper slopes of Mauna Loa as seen from summit of Mauna Kea; note very gentle slopes of Loa, and two cinder cones (explosive vents) in foreground.

FIG. 7.—View of Loa from summit of Hualalai; clouds lying at elevation of 7000–8000 ft.; note xerophytic vegetation in foreground.

Haleakala, and lastly Hualalai, the smallest of the four mountains; (3) the summits are marked by volcanic vents; either an active crater (Loa); or an extinct caldera (Haleakala); or great numbers of cinder cones (Kea); or by innumerable pit craters and cinder cones (Hualalai); all of these are large and tangible evidences of the earth forces by means of which the mountains were built up to their present height; (4) the mountains rise directly and gradually from the sea, without intervening lowlands or plateaus; (5) the

FIG. 8.—Cinder cones on floor of Haleakala caldera; at extreme upper left are some silver sword plants (*Argyroxiphium sandwicensis* var. *macrocephalum*).

slopes and flanks of each mountain are covered by thick blankets of lava, cinders, and ash, which in the arid summit and leeward regions have undergone little or no erosion; (6) each mountain has a lower windward region which receives heavy precipitation; this rain, amounting to several hundred inches per annum in many localities, has caused the rapid decay of the lava flows in these zones and has covered the flows with luxuriant rain forest; the original flow structure is obliterated beneath heavy beds of soil and vegetation. This paper does not include the humid areas.

Cinder cones

The slopes and summits of all four of the great mountains are thickly sprinkled with cinder cones (fig. 9). These vary in height from 200 to 1000 ft., with very steep slopes of 30–40°. They are composed of volcanic ash, cinders, scoria, and other ejecta, and are frequently strewn with volcanic bombs and other lava blocks. These cones are most numerous on Kea and Hualalai; they are plentiful in the caldera of Haleakala and on the leeward slopes, and are by no means infrequent on the broad flanks of Loa. Many of these cones are more or less completely covered with vegetation and are conspicuous from a distance, serving as landmarks.

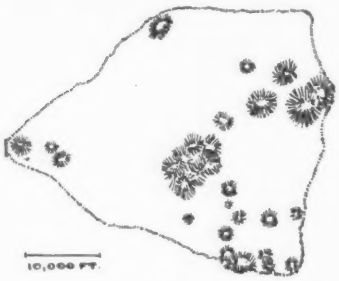

FIG. 9.—Summit plateau of Mauna Kea, showing numerous cinder cones; these explosion cones are abundant on all high mountains of Hawaii, from sea level to summit regions.

PIT CRATERS.—A second type of volcanic vent of distinct ecological interest is the pit crater (figs. 10, 11). This is typically a circular pit, its mouth flush with the surrounding country, its walls vertical or funnel-shaped, and its floor littered with volcanic débris. In diameter these pits vary from a few feet (200–300 ft. in the case of the smaller ones) to several miles in the case of the gigantic pits of Kilauea and Loa. The pits of greatest botanical interest are those of intermediate size, namely, 100–300 yards in diameter and of similar depths. There are many pits so deep and narrow that no floor is visible from the rim.

The pit craters occur indiscriminately in the rainy forest zones and on the barren slopes and summits. In the former case they are densely filled with trees and jungle litter; their mouths are often hidden by vines and other vegetation, and they constitute a serious menace to the traveler and to livestock. Those that occur in the arid sections are of particular botanical significance, as their steep walls prohibit invasion by cattle and goats, and the vegetation within them is unmolested. Thus they constitute botanical

FIG. 10.—Floor of pit crater, close to Kilauea, fissured in mosaic manner with remarkable regularity; although nearly 40 years have passed since last eruption, there has been practically no plant invasion in this crater, due to its unfavorable situation.

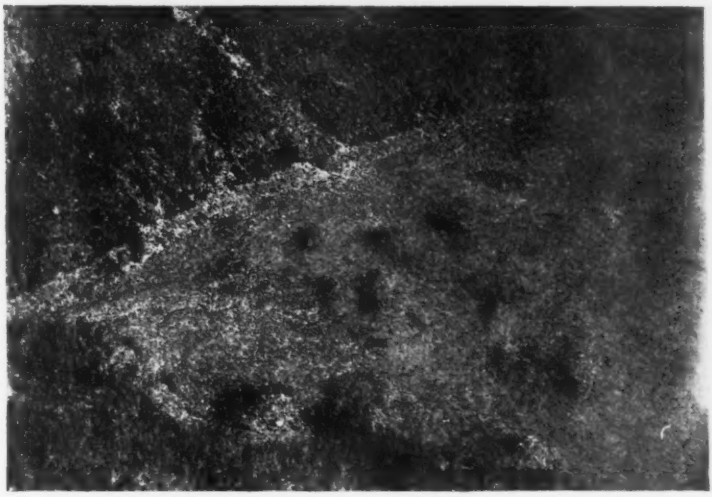

FIG. 11.—Floor and wall of pit crater close to Kilauea, largely covered with *pa-hoe-hoe;* walls covered with *Metrosideros polymorpha,* 10–20 ft. high.

oases in otherwise barren country and may be compared with the *kipukas* in the *a–a* flows. Many remnants of the primitive flora are today making their "last stand" in these tiny areas where they are protected from wild livestock, the greatest enemy of the indigenous vegetation. Finally, the conditions of shade and moisture

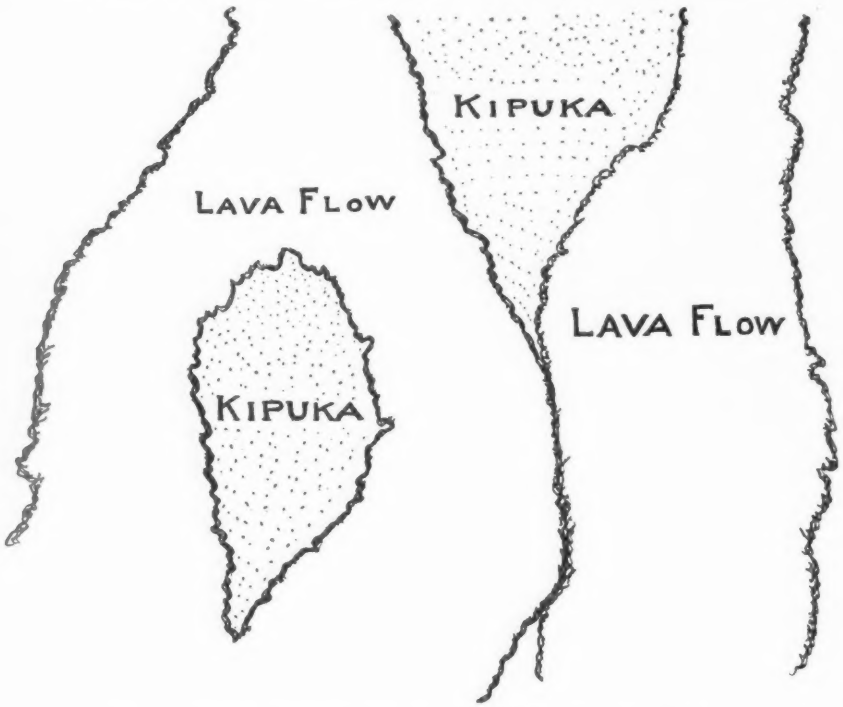

FIG. 12.—Diagram illustrating formation of kipuka in midst of lava fields.

are more likely to be favorable in the pits than on the exposed open lava flows, and the plants in the pits exhibit more normal growth forms than those in the open.

KIPUKAS.—This Hawaiian word, meaning an oval hole or depression, is a convenient designation for small areas that, owing to minor topographical irregularities, have escaped being covered by the lava flows which surround them (fig. 12). The flow may be

split or deflected so that these small patches of forest remain unscathed. Like the pit crater, the kipuka is often a botanical garden in the midst of an arid waste land.

The lava which surrounds the kipuka, and which may be 15–30 ft. higher than the floor of the latter, serves as a protection from wild cattle and goats. The kipukas frequently contain a very rich flora, a remnant of the original forest cover. These patches are usually of very limited area, not more than 2 or 3 acres, and are sharply limited by the impinging lava beds. The soil within the area is usually deep, black, and rich, and of great antiquity. There are hundreds of these kipukas on the lower slopes of the great Hawaiian volcanoes, but only those in the arid regions retain their individuality. Those in the humid regions are hidden under the rain forest.

PUU WAA-WAA.—An ancient cone of minor topographical importance, but of extreme interest from the standpoint of the geological and botanical history of the archipelago, is Puu Waa-waa, in North Kona, Hawaii. This cone is about 6 miles north of the summit of Hualalai, near the Loa flow of 1859. Its elevation is about 3300 ft. above sea level. It is 500 ft. high, with steep, deeply fluted sides. The numerous erosion ravines which radiate from the summit and produce this corrugated appearance (the native name means "fluted hill") are 50–75 ft. deep. The cone is composed of volcanic ash and cinders, and exhibits the quaqua-versal structure of the typical explosive cone. It has been deeply encircled by lava streams from Hualalai and Loa.

Studies by CROSS[2] of the lavas which underlie Puu Waa-waa have demonstrated that these lavas are trachytic, and vastly older than the basaltic lavas which now largely cover them. This hill is undoubtedly a vestige of an ancient island mass now submerged beneath newer lava. Botanical explorations by ROCK have strikingly confirmed the antiquity of the Puu Waa-waa region as contrasted with the much younger regions which surround it. Many evidences of a primitive flora have been found, a flora that has largely disappeared from other portions of this

[2] CROSS, WHITMAN, An occurrence of trachyte on the island of Hawaii. Jour. Geol. **12**:510–523. 1904.

island. The Puu Waa-waa region, like some of the pit craters and kipukas, is a botanical oasis in the midst of a desert and harbors much material of unquestionable antiquity.

VOLCANIC DUST.—In order to treat comprehensively the ecological aspects of the lava regions, it is necessary to include a statement concerning volcanic dust (fig. 13). The Hawaiian volcanoes have

FIG. 13.—Pumice fields, Kilauea volcano; chief plants, *Metrosideros polymorpha* and various xerophytic species; white patches in foreground, lichens; in distance, to right, is ohia forest, *Metrosideros polymorpha*.

been conspicuously quiescent in their activities during historic times; the outpourings of lava have been relatively gentle and non-explosive. There is much evidence, however, which indicates tremendous explosive eruptions at various periods in the history of the volcanoes, and at least one of these (Kilauea, 1790) has fallen within historic times.

Among the most abundant of the varied products of these explosive eruptions, in the Hawaiian Islands as in the case of volcanoes generally, is volcanic dust. Extensive deposits of dust

occur on the leeward slopes of Haleakala and in the caldera itself; on the leeward slopes of Kea and Loa; and great beds to the leeward of Kilauea. Perhaps the largest area is in the Ka-u district, where, according to HITCHCOCK,[3] it covers "an area of 300 sq. mi." It is not within the province of this paper to enter into any detailed account of these dust deposits, but two important floristic relations may be enumerated: (1) the obliteration of any vegetation that may have occupied the region previous to the deposit; (2) the thick layer of ashes, if rainfall or irrigation be sufficient, forms a rich and mellow soil and transforms what would otherwise have been lava waste land into productive country. The plantations and ranch lands of Ka-u owe their origin to this. It may be pointed out, in conclusion, that similar deposits of volcanic ash, of great area and thickness, occur in Central America, Mexico, the Sierra Nevadas, the Great Basin, Utah, Montana, South Dakota, Nebraska, Kansas, Washington, Oregon, Alaska, Canada, and many other places.

Ecological factors

SLOPE.—There is considerable variation in the gradient of the various high mountains, but on the whole it is remarkably gentle. Loa has a deceptively gentle slope, averaging 4–6° and not over 8° at the steeper places. Its outline against the sky is that of a very much flattened dome, or "whaleback." The slopes of Kea and Haleakala are more abrupt, usually about 12°, but sometimes as high as 15°. Hualalai is the steepest of the 4 mountains, particularly near its summit, with an average slope of 14–18°. The cinder and ash cones have slopes which lie at the critical angle for material of this character, namely, 30 or 40°. The mountains are all relatively young and have not been carved by deep, precipitous-walled amphitheaters of erosion, as have the mountains of Kauai, Oahu, eastern Molokai, and West Maui.

PRECIPITATION.—The only comprehensive records of rainfall in the Hawaiian Islands are those made by the United States Weather Bureau and the United States Hydrographic Survey. The records of the former are collaborated from the reports of

[3] HITCHCOCK, C. H., Volcanoes of the Hawaiian Islands, p. 153.

about 50 observers, scattered at various points on the islands. As these observers are stationed in or near human settlements, and as these settlements are situated in regions of at least moderate rainfall, it happens that there are no records covering the areas which form the central theme of this paper. The great upper slopes of Loa, Kea, Hualalai, and Haleakala, having a total area much greater than that of the peripheral lowlands, are uninhabited waste lands and without meteorological data comparable to that of the agricultural lowlands.

The Hydrographic Survey, interested primarily in the rain sections and the streams, has naturally avoided the great arid and streamless areas which are considered in this paper. Hence it is not possible to present extensive tables showing accurately the precipitations on these arid districts.

It is necessary to emphasize the importance of the trade winds as the rain-bearing winds of the islands. These winds blow from the northeast almost continuously through a large portion of the year. The main axis of the archipelago lies from northwest to southeast, so that the islands lie across the path of the trades, and hence develop strongly differentiated windward and leeward climates. The warm trades sweep across vast stretches of ocean before reaching the islands, and are consequently saturated with moisture. Upon striking the cool mountain slopes very heavy precipitation ensues, often totaling several hundred inches.[4] In this zone the luxuriant rain forest reaches its finest development. The leeward slopes, however, are robbed of this torrential rain; the winds that reach them are usually dry and parched, and the climate is arid or semiarid.

Snow and ice.—The high mountains of Maui and Hawaii are often snow-capped. This is particularly true of Kea, literally the "white mountain," which is prevailingly snow-crowned from November to March and intermittently at other seasons. At the season of greatest snowfall the snow line often reaches down as low as 9000 ft.; at other seasons there are frequently extensive patches of snow at the higher levels. Near the extreme summit

[4] The greatest annual precipitation officially recorded in the Hawaiian Islands is 561 inches, in 1916, on Waialeale, Kauai, by the Hydrographic Survey.

of Kea, at an elevation of 14,000 ft., is a small perennial pond, Wai-a'u, about 125 ft. in diameter. This pond is situated in an ancient crater basin and is fed by the melting snow. It is frozen during a major part of the year, even in midsummer. Ice occurs in the deep fissures and caverns in the neighborhood of the summits of Kea and Loa throughout the entire year, and during late winter it is relatively abundant.

SUMMIT REGIONS.—The treeless character of the summits has already been mentioned. The timber line is very low, indeed unusually low as compared with that of mountains in other parts of the world. HALL'S[5] explanation so accurately summarizes the local conditions that it is reproduced herewith:

> Elevation has put a sharp limit to the forests on the islands of Hawaii and Maui at from 6000 to 8000 ft. This leaves very large areas of Mauna Loa, Mauna Kea, Hualalai, and Haleakala devoid of forest, and they have always been so. The mountains of the other islands, being under 6000 ft., are forested to their summits. Six to 8000 ft. is a surprisingly low timber line, considering the favorable conditions of soil, moisture, and temperature which prevail at that altitude in Hawaii. The sufficient reason seems to be that the species composing the native forests are all representatives of the torrid zone, and in these islands, which lie right at the edge of the Tropics, find their limit at the low altitude named.

SEEPAGE.—The physical structure of the lava flow is such that seepage takes place with extreme rapidity, and in the typical flow country there is absolutely no surface water. This abnormally high percolation greatly heightens the physiological aridity of the lava as a substratum for plant life. Both the *a-a* and the *pa-hoe-hoe* types of lava are highly ramified with crevices, caverns of all sizes, and long tunnels or lava "tubes." Thus a vertical section of the mountain would reveal a copiously spongy texture, with large caverns sloping toward the sea. DANA'S[6] account may be appropriately quoted in this connection:

> Over the leeward sides . . . . where rains are infrequent, a black desert everywhere prevails, and there is, with rare exceptions, only an alternation between the smoother fields of cooled lava and the rougher districts of scoria. Yet over the barest fields there is always a sprinkling of verdure, growing

[5] HALL, W. L., Forests of the Hawaiian Islands. 1904 (p. 16).

[6] DANA, J. D., Geol. U.S. Explor. Exped. **10**:1849 (pp. 159–160).

from the many crevices or cavities. Whatever showers fall on this portion of Hawaii are at once absorbed by the cavernous rocks; and consequently through its whole extent, south and east, there are not two permanent streamlets. Water is to be found only in caverns; and often a journey of some miles must be taken by the villager to supply himself for his daily consumption. All the caverns about the lower parts of the mountains have been well explored for this necessary of life.

There is probably no other region in the world where rainwater disappears with greater rapidity than on the leeward slopes of the Hawaiian Mountains. The honeycombed lava flows swallow it up, and convey it to the sea through deep subterranean channels. Thus the aridity of the lava country is compounded by 3 factors: low precipitation, high evaporation, rapid percolation.

EVAPORATION.—An ecological factor of probably greater importance than either precipitation or percolation is that of high evaporation, which characterizes the Hawaiian flows, as it does all arid regions. This very high evaporation is strongly productive of xerophilous structures and is probably more potent than any other single factor.

The lava flow

In order to elucidate the structural peculiarities of the lava country as related to plant life, a brief synopsis of the formation of a typical flow may be presented. This is adapted from HOBBS'S[7] account.

The lava either quietly melts its way to the surface at the time of outflow, or else produces one or more fissures for its egress to the accompaniment of vigorous local earthquakes. In either case, if the lava issues at a point far below the crater, the hydrostatic pressure causes gigantic lava fountains to arise at the point of outflow. The fluid, incandescent rock shoots up to heights which range from 200 to 700 ft. or more above the surface. In the 1852 eruption of Loa a fountain of lava 1000 ft. broad rose to a height of 700 ft. A certain proportion of this fluid lava is sufficiently cooled to consolidate while traveling in the air, and upon falling it builds up a cinder cone. This cone becomes a location

[7] HOBBS, W. H., Earth features and their meaning. Macmillan. 1912 (pp. 110–111).

monument at the place of discharge. Cones of this sort are plentiful on the slopes of Loa and Kilauea. From this outlet the lava begins its journey down the slopes of the mountain. The surface quickly freezes over and produces a tunnel, beneath the roof of which the fluid lava flows with comparatively slow further loss of heat. It empties its own tunnels, and in this way the long lava tubes, beneath the flows, are formed. The great lava streams that flow down the side of Loa sometimes attain a length of nearly 50 miles, and occasionally enter the sea. They are often 2 or 3 miles broad. DANA estimated the 1852 flow to contain over 10,500,000 cu. ft. of lava. The low angle of slope presented by the flanks of the mountain, and its nearly flat summit, are due to the tendency of the sheet of liquid rock to travel far and spread widely before cooling. It is by the successive additions of such sheets that the mountain has been built up.

It is of interest to note RUSSELL'S[8] statement concerning the great Columbian lavas of the Northwest, which cover an area of 200,000–250,000 sq. miles. He points out that this is "not one vast flow, but is composed of many independent sheets, which are sometimes separated by land surfaces containing the stumps of trees and even huge trunks buried in lapilli and now thoroughly silicified."

SURFACE OF LAVA FLOWS.—There are two principal types of lava forming the Hawaiian flows, which determine the general surface and structure of the flow: *Pa-hoe-hoe*, the native word for smooth or shining, designates the smooth pavement type (figs. 14–17). The crust is glassy and frequently quite brittle. Hummocks or mounds are frequent, due to the rapid cooling of the surface. Some of these mounds are quite small, others may be 30–40 ft. high and twice as long, the thick crustal layers being broken and heaped like "pack" ice. The surface of the *pa-hoe-hoe* is commonly of a ropy or festooned pattern. The wrinkles and furrows have their convex arcs downstream, as the velocity is greater in the center than at the sides. As the smoother, pavement-like parts of the flow cool, vertical cracks develop in every direction, forming a coarse network or mosaic pattern. The distance

[8] RUSSELL, I. C., Volcanoes of North America. Macmillan. 1897 (p. 250).

between these cracks is commonly every 2 or 3 ft. in all directions. The flow is thus broken up into irregular polyhedral blocks, which tend to separate under weathering and gravity. In old flows these cracks may become several inches wide and are commonly utilized by plants as growing places. The fresh *pa-hoe-hoe* is shining jet

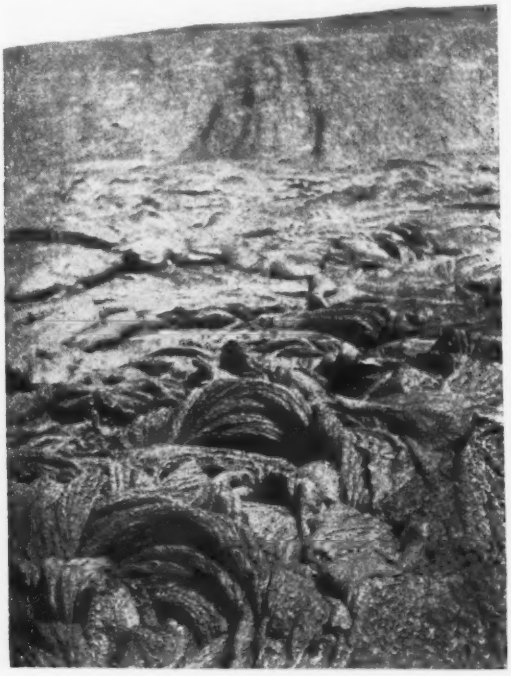

FIG. 14.—Close view of ropy or festooned *pa-hoe-hoe* on floor of Kilauea; note concave upper faces of festoons in which seeds and spores are caught and plant life first established.

black and in arid situations retains this appearance for an indefinite period. Under humid conditions, however, it weathers rapidly and becomes brown or reddish, due to the oxidation of its high iron content. On the *pa-hoe-hoe* fields the plant life occurs chiefly in the furrows or wrinkles of the ropy areas and in the numerous fissures that are abundant in the surface of the smoother areas.

FIG. 15.—Mound of *pa-hoe-hoe* lava, on floor of Kilauea crater, composed of heavy slabs of vesicular lava; surface conspicuously festooned or ropy.

FIG. 16.—Surface of festooned *pa-hoe-hoe;* note abundant lichen growth both in crevices and on protuberances; fern is *Polypodium pellucidum.*

A-a is exceedingly rough lava (fig. 18) composed of incoherent, bristling spiny blocks of all sizes, like gigantic clinkers. DANA says (*loc. cit.*, p. 162):

> They look as if the mountain had been shattered to a chaos of ruins. The fragments vary from 1 to 10,000 cu. ft. or from a half bushel measure to a house of moderate size. They are of all shapes, often in angular blocks, sometimes in slabs, and have a horrible roughness beyond conception, points and angles standing out in every direction; they lie together, touching only by their edges or points, leaving deep recesses everywhere between them.

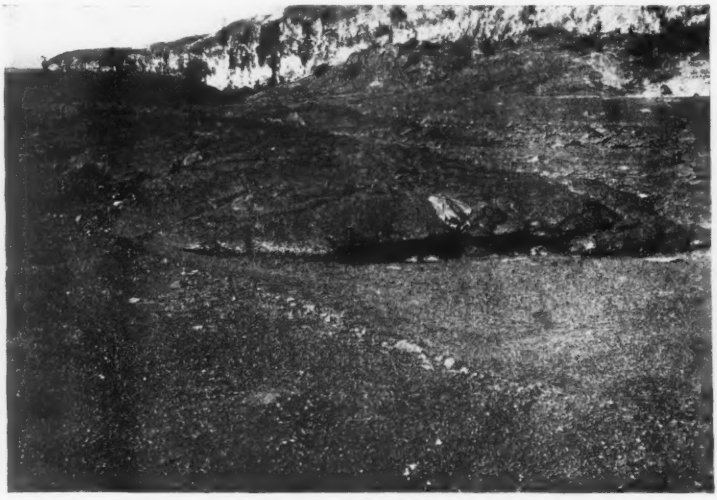

FIG. 17.—Front or end of *pa-hoe-hoe* flow in crater of Kilauea; note smooth character of surface and lobular margin; plants here and there along margin are *Vaccinium reticulatum*.

The beds are 30–60 ft. thick, with innumerable cavities between the blocks. On very old *a-a* flows the blocks and finer material have settled somewhat, rendering the entire mass more compact; the surface material is also less spiny. *A-a* flows are so rough as to be practically impassable by man or beast, and in traveling across the lava wastes one is compelled to make long detours to avoid them. The sharp cutting edges quickly destroy even the

heaviest leather boots. Horses, cattle, and goats use the *pa-hoe-hoe* as natural roadways but refuse to cross the *a-a*. It is due to this impassability of the *a-a* that plants growing upon it, or in areas surrounded by it, are protected from the devastations of herbivorous animals. Thus portions of the primitive flora have been preserved in regions where they would have otherwise been de-

FIG. 18.—Front or end of 1917 flow, which issued from flanks of Loa, composed of *a-a*, flowing over older *pa-hoe-hoe;* smoke arising from various portions of flow; note angular fragments of which *a-a* is composed, tree at lower left is *Metrosideros polymorpha*.

stroyed by wild cattle and goats. *A-a* lacks the glistening appearance of *pa-hoe-hoe* and is usually dark chocolate brown instead of black. Sometimes the reddish tint is quite pronounced. The brown and red are due to the high iron content, which characterizes all the Hawaiian lavas.

CHEMICAL COMPOSITION OF LAVA.—The following table illustrates the chemical composition of a typical Hawaiian basaltic

lava and is selected from a large series collected by H. S. WASHINGTON (U.S. Geol. Survey, Professional Paper no. 14). The

SiO_2	49.01	K_2O	0.80
Al_2O_3	16.29	TiO_2	3.93
Fe_2O_3	7.61	P_2O_5	0.49
FeO	4.89	MnO	0.27
MgO	3.62	SO_3	0.20
CaO	0.79	S	0.02
Na_2O	3.82	CuO	0.10

soils derived from the weathering of these basaltic lavas are very different from those common on the mainland of the United States. Burgess[9] states as follows:

> They are primarily basic in composition, whereas those of North America, for example, are acidic. The bases or framework of Hawaiian soils are the oxides of iron and aluminum, whereas the basis of mainland soils is silica. A glance at the following table will show these great differences better than words can express them. These figures represent averages of large numbers of soil analyses made by the "absolute" or "fusion" method. The column marked "Mainland soils" represents averages of soil analyses from almost every state in the Union and from provinces in Canada. The column labelled "Hawaiian soils" gives average figures for over 300 composite samples of soil from the leading types on all of these islands. All of these analyses were made here and under similar conditions.

	Hawaiian soils	Mainland soils
	Per cent	Per cent
Basic constituents	63.717	18.980
Acidic constituents	36.458	81.014
$Fe_2O_3+Al_2O_3$	59.240	13.250
CaO	0.698	0.830
MgO	1.242	0.771
K_2O	0.737	1.022
Na_2O	1.420	2.229

The prevailing low summit temperatures have already been noted. The annual mean temperature of Mauna Loa at the timber line is estimated by the United States Weather Bureau as 50° F. and the summit temperature as 35°. The Bureau states "in the

[9] Rept. Haw. Sugar Planters' Expt. Station, Honolulu. 1915 (p. 62).

absence of actual observations in the higher levels, a temperature decrease of 1° F. is assumed in each 320 ft. of ascent."[10] The annual mean summit temperature of Kea is given as below 30°. It should be emphasized that very much lower temperatures than these prevail during a considerable portion of the year, especially at night, and are accentuated by the high winds. During the brilliant cloudless day the black lava sheets absorb great quantities of heat, and the aerial temperatures near the ground become very high. At nightfall, however, a very rapid chilling of the air ensues, and the thermometer drops in a few hours to the neighborhood of freezing point. This sudden drop is familiar to all who have ascended the high peaks. This wide diurnal range of aerial summit temperatures is in striking contrast to the equable and monotonously invariable temperatures of the littoral regions.

TEMPERATURES OF LAVA AND CINDER FIELDS.—Reference has already been made to the low temperatures which prevail at the summit regions. Another phase of this extremely interesting ecological factor remains to be considered, namely, the comparatively high temperatures which characterize the lava and cinder fields themselves during the daytime. All of these volcanic deposits are black or very dark in color. They absorb vast quantities of heat during the uninterrupted diurnal period of insolation. Those who have traveled across the lava waste lands well know that by the middle of the afternoon the surface of the rock is distressingly hot. The surface, the rock layer immediately below it, and the aerial layer immediately above it have temperatures much higher than the prevailing aerial temperatures. This condition is similar to that reported by investigators of other desert regions. MACDOUGAL[11] notes that "the sandy soil around the roots of small herbaceous plants in the Grand Canyon, Arizona, ... exhibited temperatures as high as 148° F." It is to be further noted, as MACDOUGAL states (*loc. cit.*, p. 77), that "these extreme temperatures are met only by the roots of species spreading in the surface layers of the soil." Deep-rooted species are not so likely to be affected.

[10] U.S. Weather Bureau, Hawaii Station, Ann. Rept. 1915 (p. 2).

[11] MACDOUGAL, D. T., Botanical features of American deserts, p. 82.

No thermograph records are available for subterranean temperatures in the Hawaiian lava flows, but such will very likely correspond closely with the results obtained by Cannon.[12] In his study of the root relations of desert plants at Tucson, an almost continuous record was made of the soil temperatures at a depth of 15 cm. for the 5 years 1905–1909. CANNON states:

> The record shows an undulating record of which the curve crests correspond to the warmest for each day, and the depressions the coldest. The crests . . . . are remarkably uniform in height, as also the depressions are uniform in depth. The difference between the crests and the depressions is about 8° F., with 12° as the greatest variation. . . . . Owing to the lagging of the soil temperatures, as compared with those of the air, the maximum is not attained until about 6 P.M., and the minimum about midnight.

A careful quantitative and qualitative investigation of the root relations of the lava inhabiting species is yet to be made, but it already gives promise of yielding some valuable contributions to our knowledge of plant ecology. To quote again from MACDOUGAL (*loc. cit.*, p. 82):

> It may be said, in conclusion, that the facts disclosed as to the actual temperatures in the soil, the diurnal and seasonal change therein, lead to the belief that the differences in temperature of the aerial and underground portions of plants cannot fail to be of very great importance in the physical and chemical processes upon which growth, cell-division, nutrition, and propagation depend. The determination of the effect of differences in temperature between the roots and aerial shoots has received but little consideration from the physiologist and the geographer.

Plant invasion on lava flows

The rate and amount of invasion is chiefly dependent upon two factors: (1) proximity of adjacent vegetated regions from which invasion may take place; (2) amount of precipitation, determining the character and abundance of invading forms. A lava flow which cuts a path through the humid jungle forest is soon (30–50 years) disintegrated and overgrown. A lava flow on an arid summit slope (8000–10,000 ft.) will remain practically naked for centuries. Between these two extreme types every intermediate stage can be found (figs. 11, 19, 20).

[12] CANNON, W. A., Root habits of desert plants, p. 20.

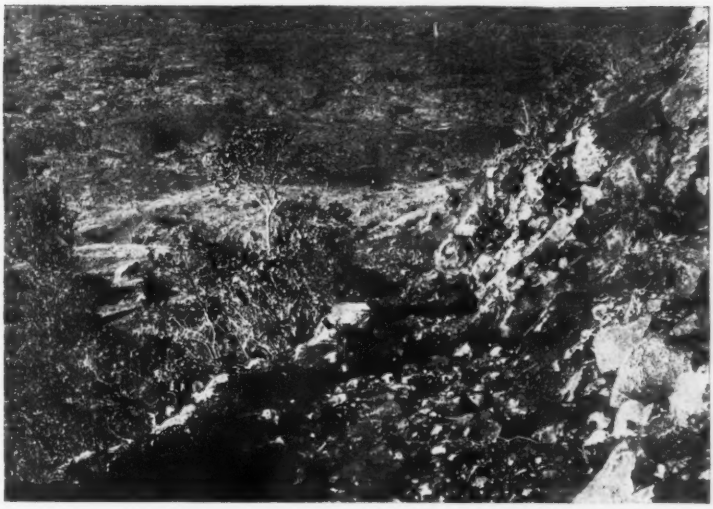

FIG. 19.—Floor of Kilauea, composed of black, lobular, hummocky *pa-hoe-hoe;* plants in foreground are *Metrosideros polymorpha, Vaccinium reticulatum, Sadleria cyatheoides,* etc.

FIG. 20.—Plant invasion on floor of Kilauea crater; near foot of wall; note that floor is smooth *pa-hoe-hoe;* ferns are *Sadleria cyatheoides;* scrubby trees near top of slope are *Metrosideros polymorpha.*

In 1912 FORBES[13] published some preliminary observations of plant invasion on lava flows. His principal findings, which coincide with the observations of the writer, may be summarized as follows:

1. Lichen flora is much more abundant on the *a-a* than on the *pa-hoe-hoe* and develops on the former at a much earlier date than the latter, other conditions being the same.

2. Ferns (such as *Polypodium* and *Sadleria*) and phanerogams (such as *Metrosideros* and *Sophora*) do not establish themselves upon the *a-a* until long after they have established themselves upon the *pa-hoe-hoe*, other conditions being the same.

3. The species occupying a recent flow are the same as those occupying older flows in the immediate vicinity.

4. Soil is formed on the *pa-hoe-hoe* at a much earlier date than on the *a-a*.

5. *Acacia koa*, a phyllodious species adapted to semi-xerophytic conditions, is the prevailing tree in the leeward upper forests of the middle zone, finally establishing itself upon the ancient flows as the dominant and final type.

Altitudinal ranges of lava flow species

Horizontal zonation with reference to altitude is strongly developed on the slopes of the Hawaiian mountains. As one ascends a great volcano like Loa or Kea, one finds pronounced changes in the vegetation with every thousand feet increase in elevation. From the standpoint of this paper the following large zones or belts may be recognized: lowland (littoral to 1500 ft.), lower forest (1000–2000 ft.), middle forest (1800–6000 ft.), upper forest (6000–9000 ft.), summit (9000–nearly 14,000 ft.). The summits of Kauai, Oahu, Molokai, West Maui, and Kohala rise to 4000–6000 ft. only and are very boggy. They are considered in another paper.[14] The point must be emphasized that there is a very considerable variation in the altitudinal limitations of these zones on the mountains of the different islands and on different slopes of the same mountain. In some regions the upper forest

[13] FORBES, C. N., Plant invasion on lava flows. Occ. Pap. Bishop Mus. 1912.

[14] MACCAUGHEY, VAUGHAN, Vegetation of the Hawaiian summit bogs. Amer. Bot. **22**: 45–52. 1916.

may cease at 6500 ft., in others the lower forest may extend almost to sea level; the figures must all be interpreted with considerable latitude for local deviation.

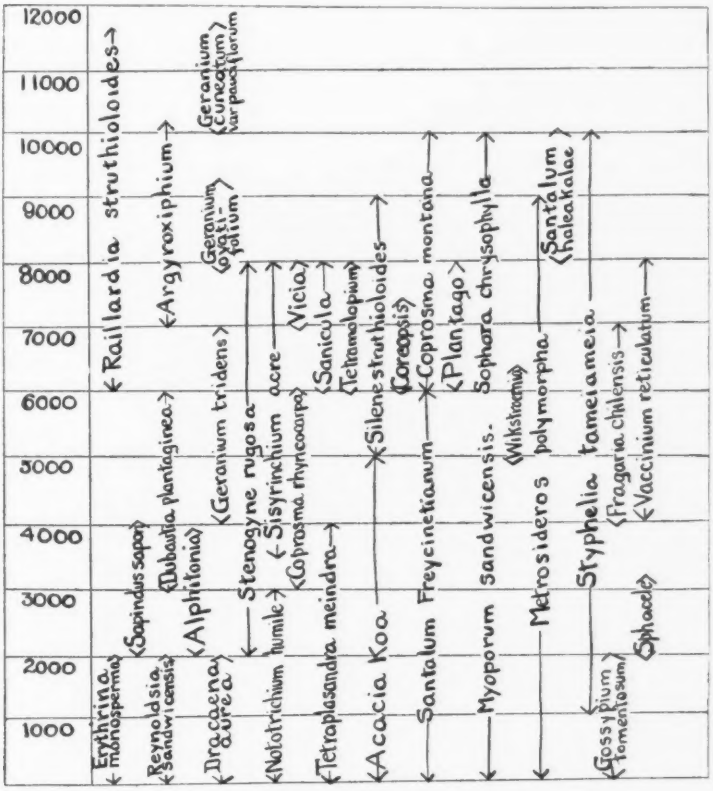

FIG. 21.—Diagram showing altitudinal ranges of some representative plants of lava flow country; figures indicate feet above sea level.

Upon classifying the lava flow species with reference to their altitudinal ranges (fig. 21), it is significant to note the great number of ranges and the fairly close adherence of each species to its range. Three general types of range may be cited: (1) wide-ranging species (*Metrosideros polymorpha*, *Sophora chrysophylla*, *Myoporum*

sandwicensis); (2) species with moderate range (*Charpentiera obovata*, *Daucus pusillus*, *Gossypium tomentosum*); and (3) species with a very narrow range (*Argyroxiphium virescens.*, *Geranium* spp., *Straussia* spp.).

Xerophytic characters of lava flow plants

PUBESCENCE.—Of the 182 species listed as occurring on the lava flows, 62, or 33 per cent, are characterized by coatings of hairy or woolly tomentum. The pubescence may cover the under surfaces of the leaves, the entire leaves, the young shoots, the inflorescences, or all aerial parts of the plant. The most pronounced examples of tomentose envelopment occur in the following genera: *Argyroxiphium*, *Gnaphalium*, *Chenopodium*, *Sida*, *Gossypium*, *Nototrichium*, *Waltheria*, *Abutilon*, *Geranium*, *Lobelia*, and *Plantago*. The point must be emphasized that with many indigenous Hawaiian plants there is exceeding variability as to pubescence; plants of the same species from various localities will show every gradation from perfectly glabrous to very hairy. This variation does not give evidence of intimate association with ecological habitat, although in a general way the glabrous forms characterize the rain forest and the pubescent forms the more arid situations. There are many exceptions to this rule, however, and a very considerable proportion of the pubescence seems to be without obvious ecological significance.

WAXY OR VISCID EXCRETIONS.—These are much less prevalent than the pubescent or coriaceous protections. Typical instances are *Argemone mexicana*, *Dodonea eriocarpa*, *Gardenia Brighami*, *Pisonia sandwicensis*, *P. inermis*, *Plumbago zeylanica*, *Raillardia* spp., *Sphacele hastata*, *Styphelia* spp., *Tetramolopium* spp., *Vaccinium* spp., *Myoporum* sp.

THORNS AND PRICKLES.—A small number of the lava flow plants are thorny or prickly; the condition characterizes introduced weeds rather than the indigenous vegetation, as shown by the following:

	Prickly	Thorny	Total
Indigenous	4	1	5
Introduced	4	5	9

Acacia Farnensiana, *Amaranthus spinosus*, *Argemone mexicana*, *Caesalpinia Bonducella*, *Cyanea solanacea* var. *quercifolia*, *Rubus hawaiiensis*, *Sida spinosa*, *Solanum incompletum*, *Opuntia tuna*, *Lantana camara*, and *Prosopis juliflora* are representative plants of this class (fig. 22).

FOLIAGE MINUTE OR SCALELIKE, or showing strong xerophilous modification.—*Acacia koa* and *A. koaia* (phyllodia), *Exocarpus Gaudichaudii*, *Portulaca sclerocarpa*, *Silene struthioloides*, and *Styphelia* spp. are examples of very small foliage. *Cassytha filiformis* and *Viscum articulatum*, two parasitic plants, have minute or vestigial leaves.

DECIDUOUS HABIT.—The deciduous habit is quite rare among Hawaiian plants, either in the rain forest or on the lava fields. Only 3 deciduous species occur on the lava flows, namely, *Erythrina monosperma*, *Sapindus saponaria*, and *Reynoldsia sandwicensis*.

DECUMBENT, STRAGGLING, OR VINELIKE HABIT.—A very large number, nearly 60 in all, or 33 per cent, of the lava flow plants are either habitually prostrate or decumbent, or assume these growth-forms on the lava. Genera containing representative species of these habits are *Abutilon*, *Argyreia*, *Boerhaavia*, *Caesalpina*, *Capparis*, *Cassia*, *Chenopodium*, *Cocculus*, *Embelia*, *Euphorbia*, *Fragaria*, *Gossypium*, *Ipomoea*, *Lepidium*, *Lipochaeta*, *Meibomia*, *Mucuna*, *Osteomeles*, *Plumbago*, *Portulaca*, *Raillardia*, *Ranunculus*, *Rubus*, *Rumex*, *Scaevola*, *Sicyos*, *Sida*, *Solanum*, *Stenogyne*, *Styphelia*, *Tetramolopium*, *Vicia*, *Vigna*, and *Wikstroemia*. Compact basal heads or rosettes are formed by such plants as *Argyroxiphium* spp., *Gnaphalium* spp., *Plantago pachyphylla*, *Sisyrinchium acre*, *Sonchus*, etc.

SUCCULENCE.—This typical xerophytic character is relatively uncommon in the lava flow flora. The few examples are mostly introduced weeds, as *Portulaca*, *Opuntia*, *Bryophyllum*, *Chenopodium*, *Sonchus*. Lignescence, representing the other extreme of structural adaptation to aridity, is the dominant condition.

HIGH PERCENTAGE OF LIGNEOUS FORMS.—Upon examining a tabular statement of the habital characters of the lava flow flora, one is immediately impressed by the high proportion of ligneous and semi-ligneous forms. Over 70 per cent are woody, and this

proportion would be heightened if a number of herbaceous perennials with woody bases or stocks were included. This ligneous character is not confined to the lava flow plants, however, nor is

FIG. 22.—Typical ligneous thorny species dominant in xerophytic habitats, on lava flows and coastal plains, *Acacia Farnesiana;* man is standing on explosively produced tufa strata.

it especially typical of them. A very large proportion of the indigenous vegetation in the humid forests is shrubby or arborescent.

In the Hawaiian Islands woodiness is to be interpreted, not as a xerophytic feature, but rather as a result of long continued plant growth (in terms of the individual plant) under unfavorable conditions. The low temperatures and excessive humidity of the rain forest belt are probably just as unfavorable for optimum plant growth as are the high temperatures and excessive aridity of the lava fields. Both habitats result in the production or modification of a large number of very lignescent, suffruticose, dwarfed, slow growing species (tables I and II).

TABLE I

HABITAL ANALYSIS OF THE LAVA FLOW FLORA

Class	Frequent	Rare	Total
Trees	48	10	58
Shrubs	65	2	67
Herbaceous perennials	29	4	33
Annuals	24	2	26

TABLE II

ENDEMICITY AND LIGNESCENCE OF LAVA FLOW PLANTS*

Class	Endemic	Not endemic	Total
Woody throughout	90	18	108
Partly woody	28	10	38
Herbaceous	12	24	36
Total	130	52	182

* 50 per cent of the total lava flow flora is composed of woody endemics; 80 per cent of the total lava flow flora is composed of woody and partly woody plants.

ROOT SYSTEMS OF LAVA FLOW PLANTS.—No comprehensive data are available on this interesting subject. The observations of the writer would tend to point to the comparatively deep rootedness of the woody species. The aridity of the flows has already been described. Deeply penetrating roots may be considered as absolutely essential for the existence of perennial plants on a rocky stratum as dry as the typical lava flow. The roots of such species

as the writer has had occasion to examine have in every case proved to be exceptionally long as compared with the proportions of the aerial parts. The roots run down for long distances into the fissures in the flows, and often pursue the most devious courses. The following plants exhibit this condition: *Acacia koa*, *A. Farnensiana*, *Alphitonia excelsa*, *Artemisia australis*, *Cassia Gaudichaudii*, *Cheirodendron Gaudichaudii*, *Coprosma montana*, *Dodonaea eriocarpa*, *Erythrina monosperma*, *Geranium cuneatum*, *Gossypium tomentosum*, *Lipochaeta subcordata*, *Metrosideros polymorpha*, *Myoporum sandwicensis*, *Osteomeles anthyllidifolia*, *Perrottetia sandwicensis*, *Psidium guayava*, *Reynoldsia sandwicensis*, *Rumex giganteus*, *Senecio vulgaris*, *Sida fallax*, *Sophora chrysophylla*, *Styphelia tameiameiae*, *Waltheria americana*, *Wikstroemia* spp., *Xylosma Hillebrandia*.

Sclerophyllous formations

A considerable proportion of the lava vegetation may be classified as sclerophyllous. The leaves of these species are thick coriaceous, usually with glistening, highly reflective upper surfaces. *Antidesma*, *Chrysophyllum*, *Coprosma*, *Maba*, *Metrosdieros*, *Nothocestrum*, *Osmanthus*, *Pelea*, *Pisonia*, *Pittosporum*, *Pterotropia*, *Sideroxylon*, *Styphelia*, *Wikstroemia*, and *Xylosma* are genera containing typical coriaceous-leaved species. It should be noted that Hawaii does not exhibit the extreme sclerophyllous condition, but rather a semi-sclerophylly. For example, many species with sclerophyllous foliage do not show noticeable dwarfing; indeed, they may be trees of considerable stature. In the Hawaiian Islands the sclerophyllous formations occur at the higher levels (5000–9000 ft.), and altitude seems to be a dominant factor in their origin and zonation.

AGE OF LAVA FLOW VEGETATION.—The vegetation of the lava flows is largely comprised of woody, long lived species. These acquire the aspect and habit of senility at a relatively early stage in their life cycles. The unfavorable conditions of the environment stamp themselves upon the physiognomy of the individual plants and of the formations as a whole. The woody species give every evidence of great age and slow growth. Shrubs 4–6 ft.

high show ages of 30 to 40 years; trees 15–20 ft. high, ages of 50 to 70 years; and trees of 40–60 ft. high, ages of 100 to 200 years or older. It may be stated as a general conclusion that the ligneous plants of the lava flows, like those of other deserts, attain great age and assume the aspect of senility at an early period in their lives.

Fossil trees

When a lava flow rolls down the mountain slope it may, and commonly does, meet with a grove or woodland across its path. The varying results of the encounter may be summarized as follows:

1. The forest may be entirely consumed by the lava flow, the trees beaten down and burned, and all trace of the grove wiped out by the rock sheet. This usually happens if the flow is *a-a* and is quite thick. There is abundant evidence on the slopes of Loa, Kea, and Haleakala to show that hundreds of thousands of acres of beautiful woodland have been obliterated by lava flows within comparatively recent geological time.

2. The flow, if of the *pa-hoe-hoe* type and moving quite rapidly through the grove, may only destroy the foliage, brushwood, and lesser vegetation. The large tree trunks are resistant even to the great heat of the flow. Moreover, the surface lava cools with such extreme rapidity (this is a noteworthy feature of the Hawaiian lavas) that the radiation from within is relatively slight. In this way large trunks are coated with an envelope or shell of lava which quickly cools and hardens, and forms a protective case, so that the heat from adjacent liquid lava does not reach the tree. The main mass of the lava flows on down the slope, leaving the grove spattered and jacketed with lava. Often great blobs of lava remain clinging to the larger limbs and festooning the summits of the saplings. Remnants of woodlands, exhibiting these phenomena, are not uncommon on the lee slopes of Loa.

3. The lava flow, acting under conditions like those just described, but moving more slowly, may ensheath the trees to a considerable height, for example, 20 ft. A jacket is formed as has been described, but the gradual incineration of the outer layer of wood results in a space between the tree trunk and the lava jacket. Fresh lava, under pressure, will force its way into this space, and

its heat will still further reduce the tree trunk. This process is continued until the tree is wholly consumed and the lava has filled the mold. The main flow passes on, leaving the lava trees behind. The result is a lava pillar or column, 15–25 ft. high, 2–5 ft. in diameter, and often expanded or flaring at the summit, where the trunk branched. These so-called "petrified trees" retain many evidences of their arboreal origin, and correspond somewhat in their mode of formation to the petrified trees of the west. In the Puna district, Hawaii, there are hundreds of these lava trees in the wake of ancient *pa-hoe-hoe* flows.

4. The fourth type of reaction between lava flow and woodland produces deep tubes instead of columns. The flow enters the grove and fills it to a depth of perhaps 20 ft. The rapid sheathing around the trunks of the larger trees protects them, as in the former cases, from immediate destruction. The flow in this instance, however, does not pass on and drain itself from the grove, but remains and solidifies. In the course of time the trunks decay and leave deep tubular vertical pits in the lava. The walls of these tubes are often plainly marked with the impressions of the bark of the trees which they once contained. The tubes are 10 in. to 5 ft. in diameter and 15–20 ft. deep. They are known as "tree molds," and are abundant on some of the old lava flows, particularly in the vicinity of Kilauea.

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SPEGAZZINIAN MELIOLA TYPES

F. L. STEVENS

(WITH PLATES XXIV–XXVI)

Through the kindness of Dr. CARLO SPEGAZZINI, I have received recently a number of original packages containing type specimens of *Meliola* described earlier by Dr. SPEGAZZINI. In each case the packet bore on the outside copious penciled notes concerning the specimen and careful, delicate drawings of the more significant structures. This collection of types, together with the notes and drawings in particular, are a fine commentary on the work of Dr. SPEGAZZINI. When we remember the large volume of his descriptive work and reflect that not only his types but other specimens as well are thus thoroughly and carefully annotated and figured, we are in a position more adequately to recognize the great indebtedness of mycology to him.

The drawings of the present collection have not been published, and in view of the comparative inaccessibility of most of these types, it is desirable that they should be made generally accessible to students by publication.

Permission having been received from Dr. SPEGAZZINI, Dr. ALVA PETERSON has faithfully copied for me, for publication, the most important of the drawings. Such copying was necessary, owing to the color of the paper upon which the originals were drawn, and the faintness of the penciling, which prohibited direct photographic reproduction. These drawings have been compared by me with the type material and are published herewith with such comments as seem necessary. A permanent celloidin mount[1] has been made from each specimen and, together with a fragment of the type specimen, is deposited in the herbarium of the University of Illinois. The original specimens have been returned to Dr. SPEGAZZINI at La Plata, Argentine.

MELIOLA ARMATA Speg. (fig. 1).—F. Puigg., Pug. I, no. 231; Sacc. **9**:415.

[1] STEVENS, F. L., Phytopathology **6**:367. 1916.

On coriaceous leaves, *Myrsine* (?), Apiahy, May 1888; no. 2382 (type).

The type specimen is heavily overgrown with several parasites. There is considerable variation in the character of the mycelium, which is sometimes straight, sometimes quite crooked. I have not been able to see the mycelial setae around the bases of the perithecia from which this species takes it name.

MELIOLA ARGENTINA Speg. (fig. 2).—Fung. Arg., Pug. I, no. 177; Sacc. 1:61.

On Cyperaceae, Buenos Aires, February 1880 (type).

The mycelium is very characteristic, close, dense, somewhat like *M. manca*, but distinguished by its very thick mycelial setae, which are striking, being darker and thicker than the mycelium. They are about 15 μ thick at base and over 800 μ long. The capitate hyphopodia are angular, that is, not smooth or echinulate as shown in fig. 2. The type is heavily overgrown by a *Coniothyrium*.

MELIOLA BRASILIENSIS Speg. (fig. 3).—Fung. Arg., Pug. IV, no. 116; Sacc. 1:66.

On leaves of Bignoniaceae (?), Apiahy; no. 1551 (type).

The young perithecia are surrounded by an areola of radiating hyphae. The perithecia also possess short hairs as figured and described by Dr. SPEGAZZINI.

MELIOLA CALVA Speg. (fig. 4).—F. Puigg., Pug. I, no. 233; Sacc. 9:414.

On Laurinaceae, Apiahy, August 1881 (type).

Heavily overgrown with "*Podosporium penicillium* Speg."

MELIOLA CLAVATISPORA Speg. (fig. 5).—F. Puigg., Pug. I, no. 241; Sacc. 9:422.

On leaves of Apocynaceae, Apiahy, April 1881; no. 1701 (type).

Perhaps the most striking character is in the sessile, nearly globular capitate hyphopodia.

MELIOLA CORONATA Speg. (fig. 6).—F. Guar., Pug. I, no. 175; Sacc. 9:428.

On *Luchea divaricata*, Guarapi, July 1883; no. 3847 (type).

The figure shows perithecial hairs to be more conspicuous than they usually are.

MELIOLA CRUSTACEA Speg. (fig. 7).—F. Puigg., Pug. I, no. 235; Sacc. **9**:413.

On *Drymis*, Apiahy, 1881 (type).

The mycelium forms a compact crustose colony, with the parts decidedly more crowded even than is shown in fig. 7.

MELIOLA DECIDUA Speg. (fig. 8).—F. Puigg., Pug. I, no. 240; Sacc. **9**:426.

On Convolvulaceae (?), Apiahy, April 1888; no. 2344 (type).

The capitate hyphopodia are very irregularly angular.

MELIOLA DELICATULA Speg. (fig. 9).—F. Guar., Pug. II, no. 63; Sacc. **9**:415.

On *Myrisinus*, Sierra de Peribebuy, September 15, 1883; no. 3985 (type).

MELIOLA ERIOPHORA Speg. (fig. 10).—F. Guar., Pug. II, no. 62; Sacc. **9**:413.

On *Ficus ibapoy*, Paraguay, January 1883 (type).

MELIOLA GLABRIUSCULA Speg. (fig. 11).—F. Aliq. Paul., no. 35; Sacc. **22**:48.

On Photiniae (?), Agua branca, Sao Paulo (type).

MELIOLA GLEDITSCHIAE Speg. (fig. 12).—Myc. Argent. VI, no. 1337.

On *Gleditschia amorphoidis*, Puerto Leon, Missiones, July 1909 (type).

MELIOLA GUAREAE Speg. (fig. 13).—Myc. Argent. VI, no. 1338.

On *Guarea balansa*, Puerto Leon, Missiones, August 1909 (type).

MELIOLA HARIOTI Speg. (fig. 14).—F. Guar. nonn. III, no. 78; Sacc. **11**:267; Gaill. Bull. Soc. Myc. Fr. **8**:186. 1892.

On Bignoniaceae, Paraguay, no. 1291 (type).

MELIOLA LEVIPODA Speg. (fig. 15).—F. Guar. nonn., no. 77 (p. 26); Sacc. **11**:264; Bull. Soc. Myc. Fr. **8**:181. 1892.

On *Aspidosperma quebracho*, Yaguaron, Paraguay, November 1882; no. 3589 (type).

MELIOLA LUDIBUNDA Speg. (fig. 16).—F. Guar. I, no. 178; Sacc. **9**:431.

On *Pilocarpus pinnatus*, Paraguay, January 1882; no. 3489 (type).

MELIOLA MEGALOSPORA Speg. (fig. 17).—F. Arg., Pug. IV, no. 115; Sacc. 1:67.

On *Jodina rhombifolia*, January 1888 (type).

The very coarse hyphae are quite characteristic.

MELIOLA MELASTOMACEARUM Speg. (fig. 18).—F. Puigg., Pug. I, no. 232; Sacc. 9:414.

On Melastomaceae, no. 2485, Apiahy, May 1888 (type).

The mycelium is often less straight than might be assumed from the figure. The oval hyphopodia are characteristic.

MELIOLA OBESA Speg. (fig. 19).—F. Guar., Pug. I, no. 179; Sacc. 9:421.

On Rutaceae, Piragu Bras, July 1883; no. 3834 (type).

MELIOLA OBESULA Speg. (fig. 20).—F. Guar. nonn., no. 75; Sacc. 11:262.

On Rutaceae, Caa-guaza, Brazil, January 1882; no. 3585 (type).

MELIOLA PUIGGARII Speg. (fig. 21).—F. Puigg., Pug. I, no. 228; Sacc. 9:414.

On *Rubus*, Apiahy, May 1888; no. 2722 (type).

MELIOLA PULCHELLA Speg. (fig. 22).—F. Puigg., Pug. I, no. 227; Sacc. 9:414.

On Myrtaceae, Apiahy, 1881; no. 1699 (type).

MELIOLA SAPINDACEARUM (fig. 23).—F. Guar. nonn., III, no. 79; Sacc. 11:266; Bull. Soc. Myc. Fr. 8:184. 1892.

On Sapindaceae, Caa-guazu, Brazil, January 1882; no. 3600.

MELIOLA SPEGAZZINIANA Wint. (fig. 24).—F. Guar., Pug. II, no. 64; Sacc. 9:418.

On Compositae, Paraguari, March 5, 1883; no. 3751 (type).

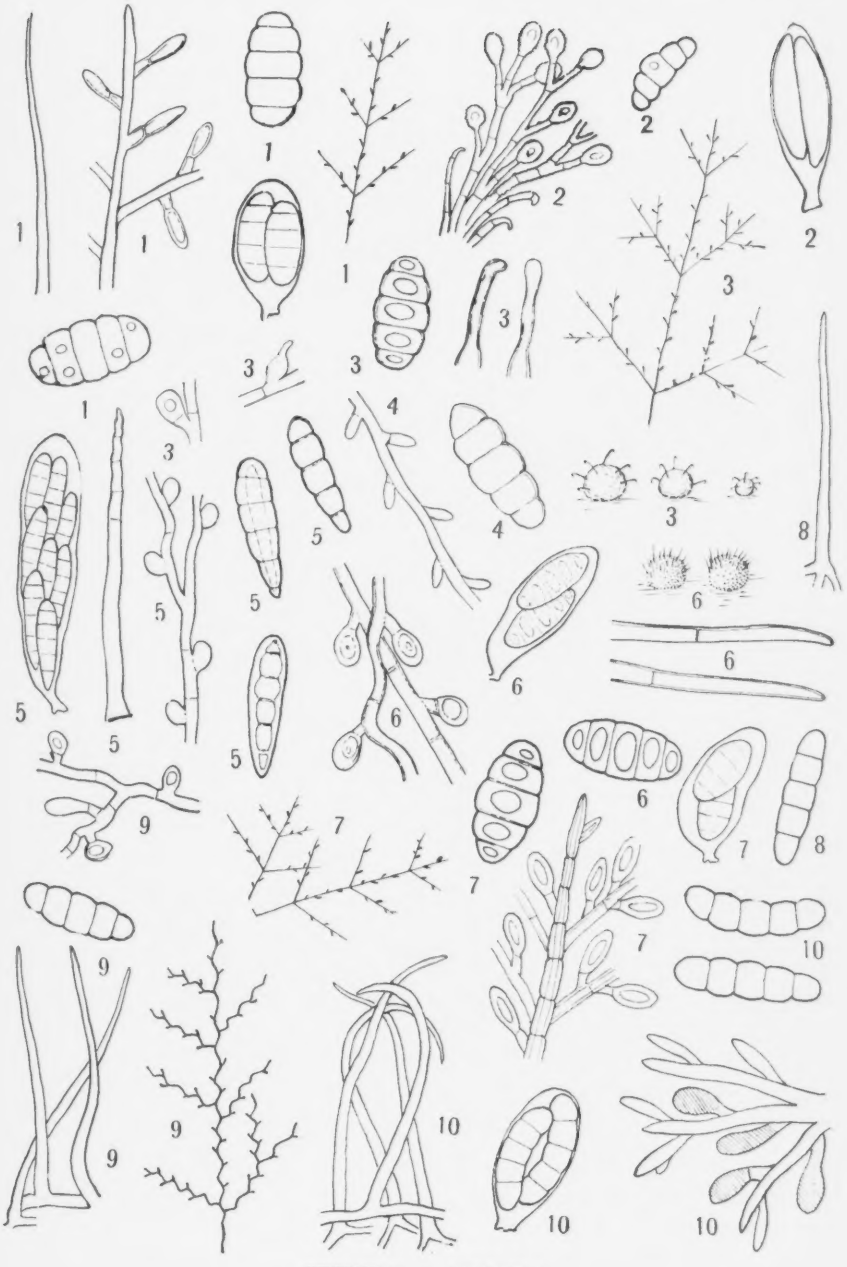
MELIOLA SORORCULA (fig. 25).—F. Puigg., Pug. I, no. 230; Sacc. 9:418.

On *Baccharis pingrea*, Apiahy, May 1886; no. 2774 (type).

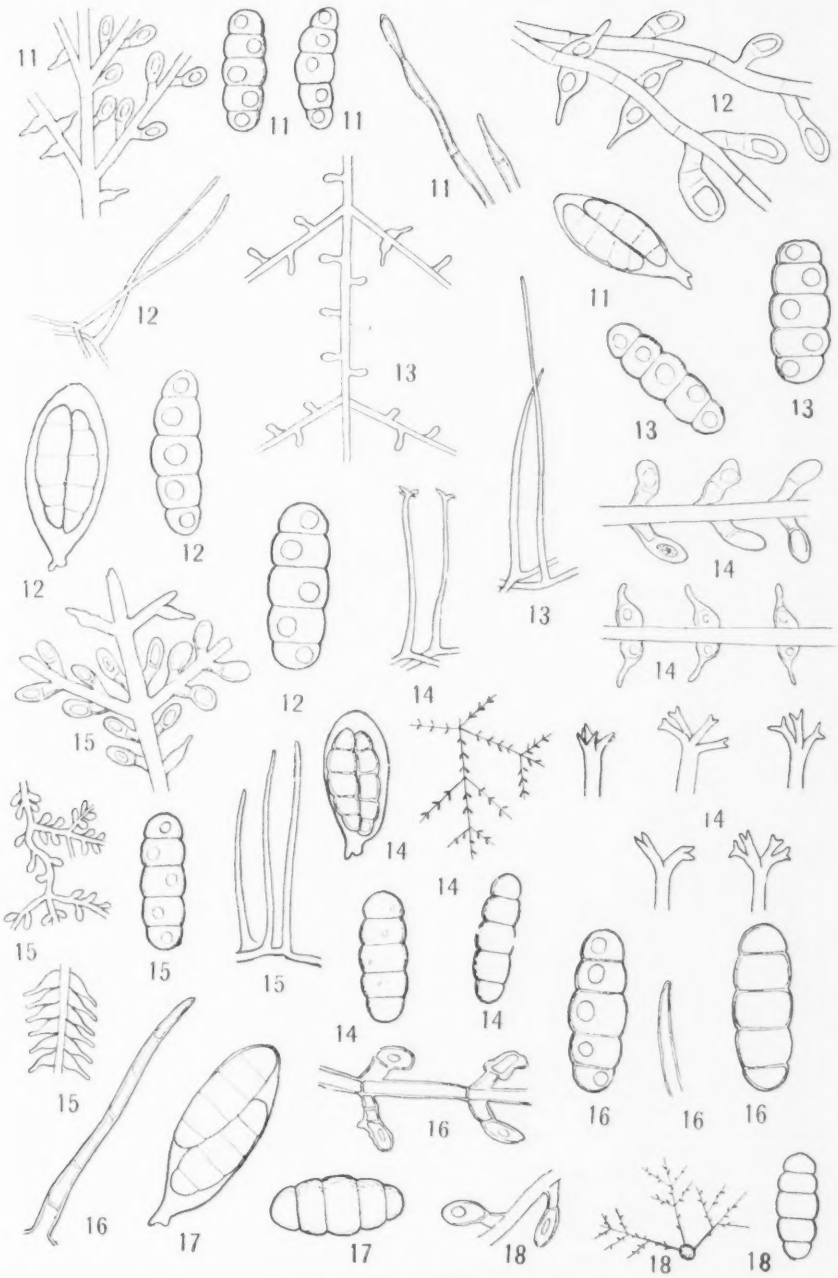
MELIOLA SUBCRUSTACEA Speg. (fig. 26).—F. Puigg., Pug. I, no. 236; Sacc. 9:430.

Apiahy, 1888; no. 2703 (type).

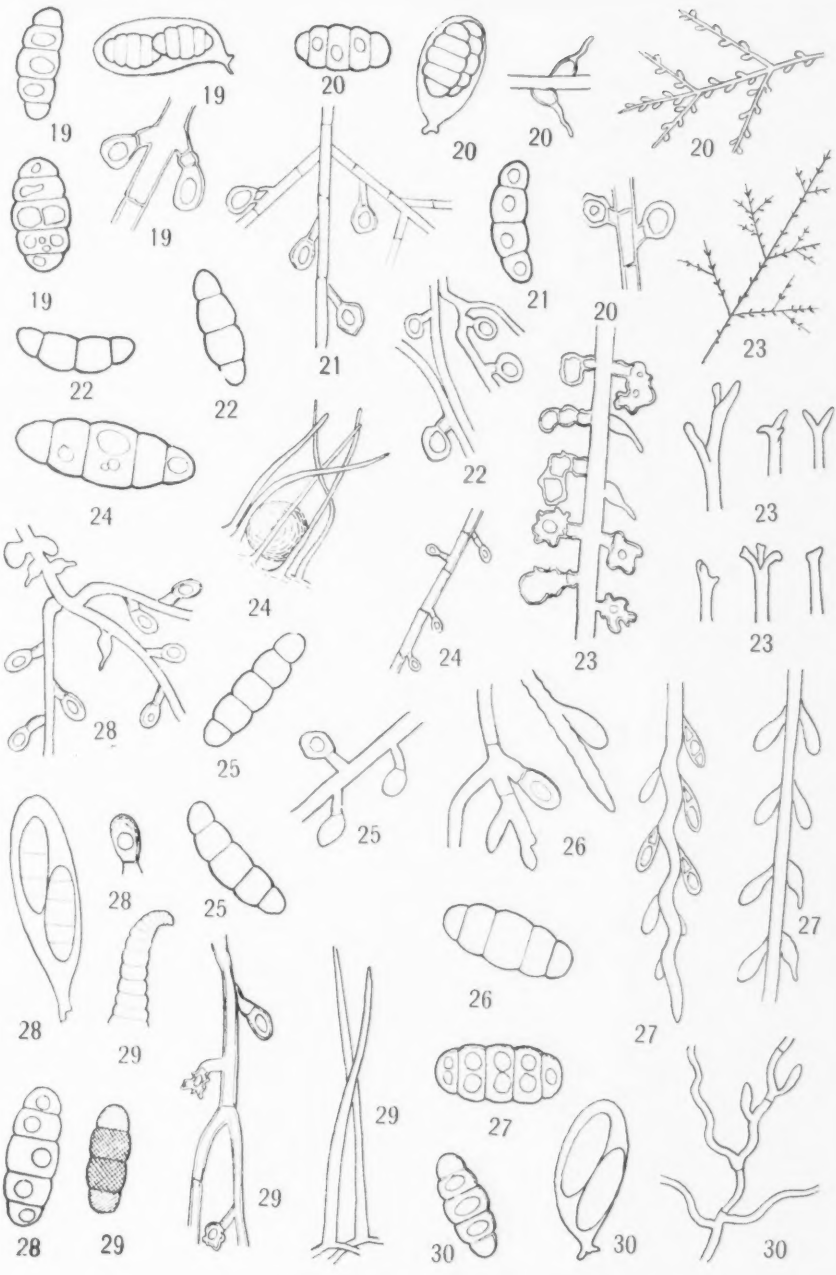
MELIOLA TABERNAEMONTANAE Speg. (fig. 27).—Myc. Argent. VI, no. 1345; Bompland Missiones.



STEVENS on MELIOLA



STEVENS on MELIOLA



STEVENS on MELIOLA

On *Tabernaemontanae historicis*, November 1909 (type).

MELIOLA TREMAE Speg. (fig. 28).—Myc. Argent. VI, no. 1346.

On *Trema micrantha*, Puerto Leon, Missiones, July 1909 (type).

MELIOLA GUARANTICA Speg. (fig. 29).—F. Guar., Pug. I, no. 176; Sacc. **9**:429.

On leaves of Guarapi, January 1883; no. 3681.

This species has been united with *Meliola ganglifera* by GAILLARD.

MELIOLA WINTERII Speg. (fig. 30).—F. Guar., Pug. II, no. 53; Sacc. **9**:424.

On *Solanum verbascifolium*, Sierra de Peribebuy, September 15, 1883; no. 3896 (type).

ABBREVIATIONS OF PUBLICATIONS CITED

Bull. Soc. Myc. Fr. = Bulletin Société Mycologique de France.

F. Puigg. = Fungi Puiggariani. Pugillus I. Boletine de la Academia Nacional de Ciencias de Cordoba. T. XI. Buenos Aires. 1889.

Myc. Argent. = Mycetes Argentinensis. I–VI. Anales de Museo Nacional de Historia Natural de Buenos Aires. 1902–1912.

F. Guar. = Fungi Guaranitici. Pugillus I and II. Analese de la sociedad Cientifica Argentina. 1883–1888.

F. Aliq. Paul. = Fungi Aliquot Paulistana. Revista del Museo de La Plata **15**:1908.

Fung. Arg. = Fungi Argentini, novi vel critici. Pugillus I, IV. Ann. Mus. Nacion. Buenos Aires. 1880–1882.

F. Guar. nonn. = Fungi Guaranitici nonnulli novi v. critici. Buenos Aires. 1891.

Sacc. = Saccardo, Sylloge Fungorum.

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STARCH FORMATION IN ZYGNEMA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 238

HELEN BOURQUIN

(WITH PLATE XXVII)

Between 1880 and 1895 much literature on the subject of starch formation appeared. At that time certain problems in regard to the origin of starch grains in algae arose which have not yet been settled. The present investigation of *Zygnema* was undertaken because its chromatophore appears to be typical of many algae, and it is so large that the possibility of error in cytological work should be minimized.

History

The most important investigations on starch formation were made by MEYER (**3, 4**). One of his conclusions is that starch is always formed by the plastid by secretion. Although he confined most of his attention to angiosperms, he believed this to be equally true for algae (**4**). He concludes that the pyrenoid is reserve protein material which is formed by the plastid and is used by the cell after its supply of starch has been exhausted. In his opinion it is homologous with the protein crystals formed in the plastids of many of the lower monocotyledons, which are likewise utilized after all the starch grains have disappeared. The plastid itself he sees as a colorless or slightly yellowish honeycombed structure ("vakuolig-poröse"), which contains chlorophyll in the form of granules. Other investigators agree that the pyrenoid is implicated in some way in the formation of starch in algae.

SCHMITZ (**7**) finds a specific pyrenoid substance which is laid down locally in the substance of the plastid in such quantities that the mass appears as a structure more or less sharply differentiated from the plastid. Although formed by the plastid, this pyrenoid substance is living and takes an active part in starch formation. He adds that in many cases the plastid forms starch without the intervention of the pyrenoid, and that pyrenoids often appear in

plastids in which no starch is formed. He thinks that the pyrenoid is homologous with the protein aleurone crystals of the lower monocotyledons, and he places the pyrenoid substance in the same chemical group as chromatin.

SCHIMPER (**5, 6**) describes the pyrenoid as a crystalline substance which rises *de novo* in the cytoplasm, and which in turn gives rise to the sheath of starch grains surrounding it. The plastids of algae always form it in the process of starch formation. If abundant, it crystallizes; if thin, it passes into starch without crystallizing and its presence cannot be demonstrated by the microscope, as is possible when it is in crystalline form. It and its surrounding sheath of starch grains are structures peculiar to algae and not homologous with any structures found elsewhere in plants. He believes that it does not belong to the same group as chromatin.

According to TIMBERLAKE (**8**) there is no differentiated chromatophore in *Hydrodictyon utriculatum*, but the chlorophyll is distributed through the whole peripheral protoplasmic layer of the cell (p. 623). Just before zoospore formation the pyrenoids disappear. They rise *de novo* when the zoospores germinate. The substance of the pyrenoid is changed into starch grains by "processes not understood." He is inclined to believe that the pyrenoid is an active independent cell organ whose function is to produce starch.

YAMANOUCHI (**9**) finds a plastid in *Hydrodictyon africanum*, a plant like *H. utriculatum* in all essential features. In its early stages the plastid is denser in the outer regions than in the center and is irregular platelike or spindle-like in form. It may produce either reserve starch grains or pyrenoids. The two are not recorded in the same plastid.

CHMILEWSKIJ (**1**) believed that the starch grains in *Zygnema* are formed wholly from the substance of the pyrenoid, plates of which extend between the starch grains, giving a starlike structure.

Miss MERRIMAN (**2**) figures the starch grains as entirely surrounded by cytoplasm except on the side abutting on the pyrenoid. Since this work of Miss MERRIMAN's has been accepted as the standard on nuclear division in *Zygnema*, it seems necessary to emphasize the fact that she makes no claim of having interpreted

the chromatophore correctly. She has figured it incidentally as it appears to the casual observer.

Material and methods

My observations were made on several species of *Zygnema*. The material came from the vicinity of Chicago and from Dr. TRANSEAU'S laboratory. It was killed in 1 per cent chromoacetic acid, part of it at 11:00 P.M. to secure cells which were dividing, and part of it at 11:00 A.M. to catch the cells in an active vegetative condition.

Filaments were mounted whole in Venetian turpentine and stained with anilin blue and Magdala red and with gentian-violet and anilin blue in order to differentiate the parts of the chromatophore. Iron hematoxylin was also used for some preparations. Most of my observations were made on the whole filaments. Many of the drawings are optical sections of whole chromatophores. The advantage in this method lies in the fact that the true sizes and relations of the starch grains and the exact extent of the pyrenoid in the chromatophore can be ascertained by focusing up and down. The use of sectioned material exclusively might lead to errors of interpretation by taking the transverse section of a grain for a small one, or by failure to see the full extent of the pyrenoids. Longitudinal and cross-sections of cells 3 μ thick were also made and were stained with gentian-violet and safranin, iron hematoxylin, and Flemming's triple stain. An 8× ocular and a 2 mm. objective were used for examining the preparations.

I wish to thank Dr. C. J. CHAMBERLAIN for much valuable help and for his many suggestions.

Description

The chromatophores lie, one on each side of the nucleus, in the middle of the cell, suspended there by means of bands of cytoplasm which radiate from them to the layer of the cytoplasm along the cell wall (fig. 1). Under low-power lenses these bands appear to be part of the chromatophore and have led writers of textbooks to speak of the star-shaped chromatophore of *Zygnema*. The chromatophore is really round or oval in shape. It is a plastid containing imbedded in its substance a pyrenoid, which lies near

the center, and starch grains which radiate out from the pyrenoid (fig. 7).

Staining differentiates the plastid from the pyrenoid and the starch grains. The plastid is stained a bright blue by anilin blue, gray by iron hematoxylin, and faintly violet by gentian-violet when the starch grains are stained very deeply violet. It is colorless when the starch grains are only faintly violet. The latter are stained a yellowish red by Magdala red and violet by gentian-violet. The pyrenoid stains red with Magdala red and safranin and dark blue with iron hematoxylin. The plastid is differentiated from the cytoplasm which surrounds it by its structure, the plastid appearing homogeneous (figs. 1, 7).

It is most easily seen in chromatophores which are dividing (figs. 17, 18), but any chromatophore in which the starch grains are not closely packed shows it. A layer of the substance of the plastid always surrounds each starch grain and the pyrenoid, thus separating the starch grains from each other and from the pyrenoid. This layer can be demonstrated even when the starch grains are most closely packed (figs. 1, 2, 3, 10).

The pyrenoid is a homogeneous structure which stains with different intensity in different parts of its mass, so that one part of it will be dark blue and another gray, or one part lighter red than another. It usually forms a compact, irregularly oval or round mass in the center of the plastid from which it is sharply differentiated. An examination of the figures will show that it may vary greatly from these shapes, but it does not extend up between the starch grains as CHMILEWSKIJ (1) believed. Staining the chromatophore with Magdala red, which stains the pyrenoid, and with anilin blue, which stains the plastid, proves this conclusively. Occasionally, when there is a large space between two starch grains, tongues of the pyrenoid extend a short way up between them (fig. 8). These tongues never reach the periphery of the plastid, come into direct contact with a starch grain, or surround one.

I have not found more than one pyrenoid in a plastid unless that plastid was about to divide, division of the pyrenoid always immediately preceding the division of the plastid (figs. 17, 18).

In the majority of chromatophores the starch grains lie radially about the pyrenoid, with their broad end toward the periphery of the plastid and the narrow end abutting on the pyrenoid (figs. 1, 2, 10). They are approximately equal in length, but vary in shape from cuneate to trapezoidal to rectangular (grains *l*, figs. 2, 3, 10, 16). Their opposing faces are straight; the outer faces are rounded or straight.

In many plastids there are minute grains in the periphery of the plastid (figs. 8, 10, 15, 16). Grains of all sizes from minute grains to the larger grains are also found. These intermediate grains are all cuneate in shape, if they lie between the larger grains, and always occur near the periphery of the plastid (figs. 8, 15, 16). Occasionally the starch grains are clustered irregularly about the pyrenoid (figs. 8, 15). In this case also the smaller grains are found in the periphery of the plastid.

Discussion

There are two opinions about the origin of starch grains in algae. The majority of investigators believe that the pyrenoid is concerned in starch formation. MEYER believes that the pyrenoid is not concerned in starch formation. The pyrenoid may be implicated in starch formation in either of two ways. Its substance may be changed into starch, that is, it may form starch by fragmentation, as SCHIMPER (**5, 6**) and TIMBERLAKE (**8**) believed, or it may be an active starch-former by secretion.

In *Zygnema* the substance of the pyrenoid is not changed into starch. This is shown by a comparison of the shape and position of the starch grains and the shape and position of the pyrenoid and by an examination of the pyrenoid itself. If the starch is formed by fragmentation of the pyrenoid, there should be such a similarity in the contour of the two that the starch grain could be fitted into the edge of the pyrenoid as the parts of a puzzle fit together. If the grains are chipped out so that they come to lie radially about the pyrenoid, bands of the pyrenoid should lie between the starch grains. Even though the pyrenoid were to grow and change shape after the formation of each starch grain,

some newly formed grains would always be found which would indicate their origin in that way.

Typically the pyrenoid forms a round mass in the center of the plastid (fig. 1). The most extreme variations in its shape are figured (figs. 2, 8, 12, 14). In no case is there a striking similarity between the contour of the pyrenoid and the starch grains, nor does the pyrenoid extend between the starch grains in such a way as to suggest that the starch grains have been cut out of the substance of the pyrenoid. Fig. 8 is the most suggestive found.

Although the pyrenoid is stained with different intensity in different parts, the whole pyrenoid stains the same color with any given stain. The narrow band of the substance of the pyrenoid connecting the halves of a dividing pyrenoid never stains deeply (fig. 18). In the vegetative plastid these light and dark areas bear no definite relation to each other or to the surrounding starch grains (figs. 2, 3, 8, 9, 11, 15). Moreover, these light and dark areas are uniformly homogeneous in structure. I believe, therefore, that they do not indicate any change in the substance of the pyrenoid; they are simply regions of different density.

Grains lying radially about the pyrenoid and varying in shape from cuneate to rectangular might be formed by the pyrenoid by secretion were the pyrenoid to form them in the periphery of the plastid and add to them centripetally, or to form them at the center of the plastid and add to them continually on the inner edge, such additions pushing them automatically toward the periphery of the plastid. The first manner of formation is impossible since the pyrenoid is always confined to the center of the plastid and in no case was seen to approach the periphery where the smaller grains of starch occur. The nearest approach to such a situation is seen in figs. 8, 14. The second possibility cannot exist because the small grains are never found next to, or near, the pyrenoid. They were found without exception in the periphery of the plastid. Since there is no indication that starch grains ever split, they could not have been derived indirectly from the pyrenoid in that way. The fact that the plastid separates the pyrenoid and the starch grains becomes significant when added to these proofs that the pyrenoid does not take part in starch formation in *Zygnema*.

Everything bears out the following theory concerning the origin and growth of the starch grains in the form. The plastid gives rise to minute starch grains in its periphery, either between the larger grains (figs. 15, 16) or entirely beyond them (figs. 8, 11). Their growth seems to be regulated by their position in relation to the larger grains and to be a mechanical matter. Figs. 5, 6, 13 show how the shapes of the grains seem to fit naturally into the place occupied. If the small grains lie between larger grains, the plastid adds to them in such a manner that they become cuneate in shape. The enlargement on the inner face continues to be more rapid lengthwise of the grain than laterally as it grows down between the grains toward the center of the plastid, so that when it attains the length of the large grains it is still cuneate. A comparison of grains *t* in figs. 3, 8, 14, 16 shows a complete gradation in the lengths of the grains from the shortest to the longest, so that a perfect series could be arranged were the grains removed from their respective plastids.

After lengthening the grain in the manner described, the plastid begins to add most rapidly to the narrow base laterally, so that the grain becomes trapezoidal and then rectangular in shape. In rare instances this basal broadening may continue until the grain is once more trapezoidal (fig. 2). Grains *l* in figs. 2, 10, 16 show every stage in the change of shape just mentioned. If the small grains are formed above larger grains, they grow rectangular or oval, pushing the grain below toward the pyrenoid. This is the unusual rather than the normal method of growth, however.

Summary

The chromatophore of *Zygnema* is a plastid containing imbedded in its substance a pyrenoid which lies near the middle, and starch grains which usually lie radially about the pyrenoid.

The pyrenoid cannot take part in starch formation because it is always confined to the center of the plastid and is separated from the starch by the plastid, and because the small young grains of starch are always found in the periphery of the plastid. The plastid therefore must form these minute starch grains.

The starch grains come to lie radially about the pyrenoid in the following manner. The plastid adds to them in such a way that they become cuneate in shape. In this manner they grow down between the starch grains already formed until they are of the same length as the large grains. The plastid then broadens them at the base until they become rectangular in shape.

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DECATUR, GA.

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EXPLANATION OF PLATE XXVII

The drawings were made by the aid of the camera lucida, the magnification being ×1040. The abbreviations used are as follows: *c*, cytoplasm; *r*, pyrenoid; *n*, nucleus; *p*, plastid; *g*, starch grain; *t*, starch grain growing in length toward center of plastid; *l*, starch grain growing broad at base; *s*, minute starch grain.

FIG. 1.—Optical section of cell showing relation of cytoplasm, nucleus, and chromatophores, and showing typical chromatophores packed with large starch grains radiating from pyrenoid.

FIG. 2.—Optical section of chromatophore showing grains of varying width at base.

FIG. 3.—Optical section of chromatophore showing grains of varying lengths and grains which vary in width of base as compared with width of outer edge.

FIG. 4.—Cross-section of chromatophore showing grains of starch in cross-section.

FIG. 5.—Same as fig. 4.

FIG. 6.—Same as fig. 4.

FIG. 7.—Optical section of chromatophore showing several smaller starch grains in periphery of plastid.

FIG. 8.—Optical section of chromatophore showing minute starch grains in periphery of plastid, a pyrenoid of unusual extent and shape, and many starch grains which vary greatly in shape and length.

FIG. 9.—Median longitudinal section of chromatophore showing several small starch grains.

FIG. 10.—Same as fig. 2.

FIG. 11.—Cross-section of cell showing chromatophore in cross-section.

FIG. 12.—Same as fig. 9.

FIG. 13.—Same as fig. 9.

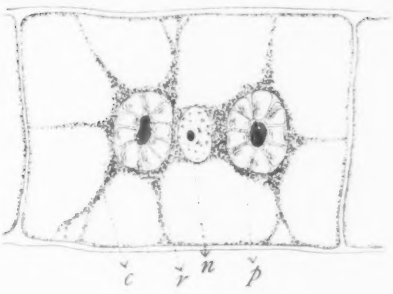
FIG. 14.—Optical section of chromatophore showing another pyrenoid of unusual shape, and starch grains of several different lengths.

FIG. 15.—Optical section of chromatophore showing many small starch grains near periphery of plastid, and large grains which differ in shape because of width of bases.

FIG. 16.—Same as fig. 15.

FIG. 17.—Optical section of plastid in process of division, showing pyrenoid after it has divided.

FIG. 18.—Optical section of plastid in process of division before pyrenoid has completed division.



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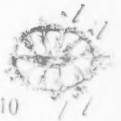

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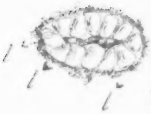

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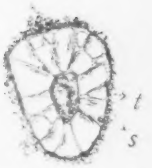

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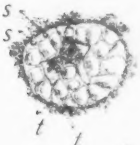

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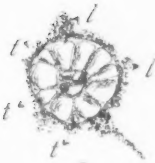

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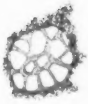

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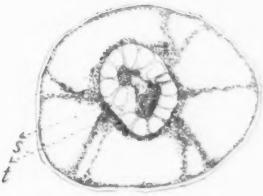

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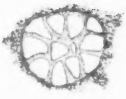

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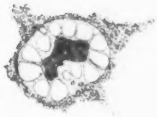

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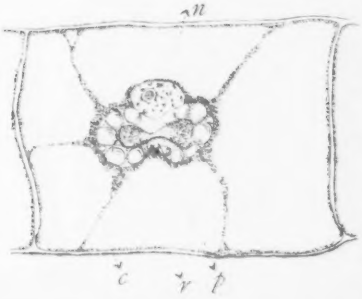

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BOURQUIN on ZYGNEMA

BRIEFER ARTICLES

APOGAMY IN PHEGOPTERIS POLYPODIOIDES FÈE, OSMUNDA CINNAMOMEA L., AND O. CLAYTONIANA L.

Apogamous embryos developed on prothallia of *Phegopteris polypodioides* Fèe, *Osmunda cinnamomea* L., and *O. Claytoniana* L. in cultures on Prantl's and Knop's full solutions and certain modifications of the Prantl's solution. About 6 months after the spores had been sown, the first cases of apogamy were observed in cultures of *Phegopteris polypodioides* on Prantl's solution with NH_4NO_3 omitted. The spores from which the prothallia developed had been collected during the summer from a plant growing on a lawn in Ithaca, New York. The plant did not appear in a normal, healthy condition, doubtless owing to the unfavorable conditions under which it was growing. After the spores were sown upon the nutrient solutions, the cultures were placed before an east window, where the conditions of light and temperature were approximately the same for all. Once each week the prothallia were transferred to fresh nutrient solutions.

The prothallia, upon which the apogamous embryos developed, were heart-shaped and developed archegonia but no antheridia. The apogamous embryo in most cases originated as a slight swelling of the archegonial cushion, either on the dorsal or ventral side, at some point near the notch or at the center of the cushion. This swelling gradually increased until a dome-shaped cellular mass was formed, from which the apogamous embryo developed. The parts of the embryo usually appeared in the following order: the leaf or leaves, root, and stem. However, in one case a root appeared before any other member. No foot was formed. In some cases, beside leaves, proliferations, either filamentous or slightly expanded at the apices, developed from the cellular mass. October 7, 1916, two series of cultures on the Prantl's and Knop's full nutrient solutions and modifications of the Prantl's solution were made. Fresh spores from the same plant at Ithaca, New York, as well as spores of the same species secured through the kindness of Dr. A. H. GRAVES from Brooklin, Maine, were used. As soon as the spores were sown upon the nutrient solutions, one series was placed in the greenhouse in bright light, while the other series was kept in the laboratory before an east window. The prothallia were not transferred to fresh solutions, but

were allowed to remain upon the original solution on which the spores had been sown. A luxuriant growth of algae developed in all of the cultures, which added to the unfavorable growing conditions.

March 9, 1917, in both series of cultures, apogamous embryos were observed on the prothallia which developed in Knop's full solution from spores collected in Maine. Archegonia were developed on many of the heart-shaped prothallia, while in some of the cultures on the smaller prothallia antheridia were present. Some of the archegonia appeared aborted. In most cases the apogamous embryos developed in the manner which has previously been described. However, a few cases of peculiar development were observed. Multicellular hairs or outgrowths formed at the base of the first leaf or leaves of the young sporophyte, or at various places on it.

On one prothallium a long cylindrical outgrowth several cells in thickness developed from the cellular mass along with the leaves of the apogamous sporophyte. As growth proceeded, this outgrowth broadened out into a one-celled prothallium-like structure, after which it again assumed the cylindrical shape bearing tracheids; at its apex it tended to return to the prothallium structure. On another prothallium an outgrowth which had developed from the notch of the prothallium and projected as a narrow process broadened at the apex, forming a slightly notched prothallium.

The only cases of apogamy on prothallia developed from spores collected at Ithaca, New York, occurred in the culture of Knop's full solution which had been kept in the laboratory. Most of the apogamous embryos originated from cellular masses formed on the prothallia, but on one prothallium a cylindrical outgrowth bearing tracheids developed from the cells in the notch. At the apex of this long cylindrical process a cellular mass was formed, from which the leaves, root, and stem of the apogamous embryo developed.

Two series of cultures of *Osmunda cinnamomea* and *O. Claytoniana* were made at the same time, in the same manner, and placed under the same conditions as the cultures of *Phegopteris polypodioides*. Apogamous embryos were observed March 9, 1917, on the prothallia in the following solutions: Prantl's full solution, Prantl's solution with NH_4NO_3 omitted, and Prantl's solution with $MgSO_4$ omitted. Some of the apogamous embryos developed from cellular masses; others originated as cylindrical outgrowths containing tracheids, from the notch of the prothallia, bearing at their apices cellular masses which gave rise to the leaves, root, and stem of the sporophyte. On one prothallium an apogamous sporophyte formed near the notch, while at its base a lobe of the prothallium

developed, on which in turn occurred an apogamous embryo. In the latter the root developed first. Only three cases of apogamy were observed in *Osmunda Claytoniana* in Prantl's solution with K_2SO_4 omitted. In two cases the sporophytes developed from a mass of cellular tissue, while the third arose as an outgrowth in the notch of the prothallium. A further study will be made of these apogamous forms.—ELIZABETH DOROTHY WUIST, *Osborn Botanical Laboratory, Yale University.*

RAY TRACHEIDS IN QUERCUS ALBA

(WITH ONE FIGURE)

In the course of a recent study of the medullary rays of the Fagaceae, the writer was impressed with the manner in which some of the fibro-tracheids in *Quercus* were associated with the rays. It is very common

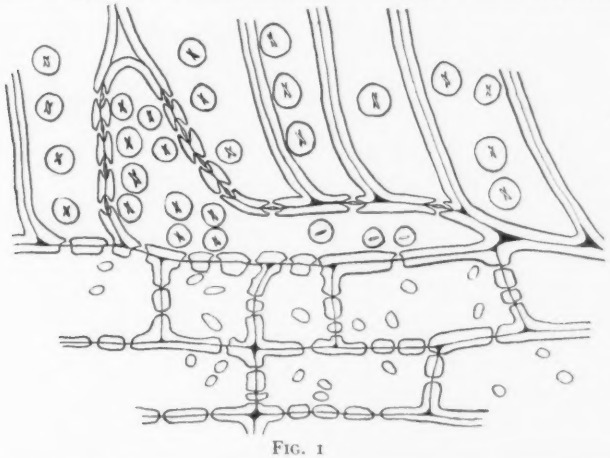

FIG. 1

to find the ends of these elements procumbent on the marginal ray cells for a considerable distance and communicating through semi-bordered pits. This condition is so similar to that found in certain coniferous woods that search was made in sections of oak wood at hand for tracheids that were distinctly radial. Fig. 1 shows a marginal ray tracheid of a uniseriate ray in normal stem wood of *Quercus alba* Linn. Another, somewhat smaller, was found in a different ray in the same section. The location is in the median late wood of the season's growth and is not in immediate proximity to a large vessel. So far as the writer is aware, ray tracheids have not previously been reported in the woods of the dicotyledons.—SAMUEL J. RECORD, *Yale University.*

CURRENT LITERATURE

BOOK REVIEWS

Physical chemistry and biology

McCLENDON[1] has performed a valuable service to biologists by organizing the more important facts and principles of physical chemistry that have to do with biological problems. These are stated briefly and concisely, and the usefulness of the book is increased by clearness in definitions. Several passages in the introduction are suggestive of helpful lines of work and interpretation.

The following paragraph from the preface suggests the viewpoint: "The purpose of this book is not to go far into physical chemistry, but to develop a tool for physiological research. Lengthy discussions of debated questions are avoided by tentatively accepting the hypothesis which fits the most facts, until a better one appears. For further discussion of any subject the reader is referred to the literature list and index. For facts, however, he is referred to nature. It is not to be hoped that theories should coincide exactly with data available at present. Even in the most exact branches of chemistry the atomic weight determinations, for instance, do not exactly coincide with the values calculated from the atomic numbers, and there seems to be some doubt as to whether lead is one element or several. How much more uncertainty there should be about physiology, where determinations are vitiated by the great variability of the material and its physiological states."

The book seems to be more from the biological standpoint and much better balanced than some other books on the relation of physical chemistry to biology that have come to the attention of the reviewer. In the introduction the author says, "Though the problems considered in this book are physiological, the methods of attack are chiefly those of the physical chemist." The book should do much toward encouraging the kind of work and thought that is neither distinctly chemical, in the sense of ignoring the structures and physical environment within which the reactions must take place in organisms, nor yet strictly biological, in the sense of ignoring any of the chemistry involved.

When the author states (p. 1) that the methods that may be applied to the interior of living cells are at present very few and concerned chiefly with the inorganic constituents, he is putting entirely too low an estimate on microchemistry as a means of investigation. It is true that this is as yet an imperfect tool, but still it is useful in a great many cases in detecting organic compounds as well as inorganic. While his statement that "modern biochemistry is therefore not yet concerned directly with the composition of normal living

[1] McCLENDON, J. F., Physical chemistry of vital phenomena. For students and investigators in the biological and medical sciences. 8vo. pp. vi+240. *figs.* 30. Princeton Univ. Press. 1917.

cells, but with their decomposition products and the exchange between the cell and its surroundings," and that from our knowledge of these "we may speculate on the composition of the cell and the changes that go on in it during functional activity," represents two lines along which productive work is being done and will continue to be done, he is leaving in the background a third line which has also proved helpful and promises still more for the future.

We might wish that the author had given more recognition to the fact that many plant processes are conditioned by the permeability or impermeability of non-living plant membranes. These, however, are very minor criticisms on a book which commends itself strongly by its many excellent features. Among the important topics discussed in the introduction are viscosity as a factor in diffusion, surface phenomena, and the relation of semipermeability to electric phenomena.

His discussion of the plasma membrane (p. 94) as a separate phase which may change with the physiological condition of the cell, and of the protoplasm as sometimes consisting of as many as four phases, in all of which partition solubility must be considered, as well as the molecular condition of each solute in each phase and in the bathing medium, leads him to the conclusion that "all of these factors make the subject of cell permeability a very complex one, no general rules without exception having been found. All we can do at present is to collect data on the permeability of cells to various substances." It is to be hoped that this will commend itself so strongly to biologists that we shall have a larger output of data and a smaller output of theories.

The following shortened chapter headings will suggest the general scope of the book: electrolytic dissociation; osmotic pressure; hydrogen and hydroxyl ion concentration; surface tension and absorption; electrolytes, non-electrolytes, and colloids; enzyme action; permeability and its changes; negative osmosis; anesthesia and narcosis; amoeboid motion, cell division and parthenogenesis; muscular contraction; blood and other cell media.

The "chemical summary" in the appendix will be very useful. The literature list includes over 1500 papers arranged alphabetically according to authors. References in the text to this list facilitate more detailed study of any desired topic. Instead of the conventional index to the text, there is an index to this literature list.—GEORGE B. RIGG.

NOTES FOR STUDENTS

Taxonomic notes.—BLAKE[2] has described a new *Rudbeckia* (*R. Deamii*) from Indiana, closely allied to *R. speciosa*.

COKER[3] has published a detailed and handsomely illustrated monograph of the *Amanita* group as represented in the eastern part of the United States.

[2] BLAKE, S. F., A new *Rudbeckia* from Indiana. Rhodora **19**:113–115. 1917.

[3] COKER, W. C., The Amanitas of the eastern United States. Jour. Elisha Mitchell Sci. Soc. **33**:1–88. *pls. 69*. 1917.

He recognizes 7 species in *Amanitopsis*, although he regards the genus as "artificial and without systematic significance," separated from *Amanita* by the absence of a single character. In *Amanita*, 27 species are described, with full discussion and citation of stations; among them there are 2 new species and 2 new varieties. The numerous plates are unusually good reproductions of fine photographs.

GARDNER,[4] in a first paper on new marine algae from the Pacific Coast, describes, in collaboration with SETCHELL, 9 new species in as many genera. *Coriophyllum* and *Cumagloia* are described as new genera.

KAUFFMAN[5] has described a new species in *Russula* (*R. ochroleucoides*) and in *Stropharia* (*S. caesiospora*) from Tennessee. They are described in connection with a list of fungi collected in Kentucky and Tennessee during September 1916.

MACBRIDE,[6] in a revision of the North American species of *Amsinckia*, recognizes 23 species, 6 of which are described as new. In further notes on the Boraginaceae, he publishes new species in *Cordia*, *Onosmodium*, and *Lithospermum*, a new variety of *Macromeria exserta*, and new combinations in several genera. In notes on the Hydrophyllaceae, the same author describes a new genus (*Turricula*) founded on *Nama Parryi* Gray, also new species in *Phacelia* (6) and *Miltitzia*, 9 new varieties, and numerous new combinations. A new species is also published in *Petalostemum*, and *Gilia virgata* and its allies (a group of 5 species) are discussed. In cooperation with PAYSON, the same author describes new species in *Arabis*, *Dodecatheon*, *Mertensia*, *Veronica*, *Castilleja* (2), and *Hieracium*, all from Idaho; and also revises series MULTIFIDI of *Erigeron*, recognizing 3 species and 7 varieties, 3 of the varieties being new.

STANDLEY,[7] in a monograph of the Mexican and Central American forms of *Ficus*, recognizes 41 species, 17 of which are described as new.

WERNHAM,[8] in continuing his studies of the Rubiaceae of the American tropics, has described *Neobertiera* and *Blandibractea* as new genera. He also presents the genus *Sipanea*, recognizing 10 species and describing 6 of them as new; also 3 new species of *Cephalanthus* are described.—J. M. C.

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[4] GARDNER, N. L., New Pacific Coast marine algae. I. Univ. Cal. Publ. Bot. **6**:377–416. *pls. 31–35*. 1917.

[5] KAUFFMAN, C. H., Tennessee and Kentucky fungi. Mycologia **9**:159–166. 1917.

[6] MACBRIDE, J. FRANCIS, Contrib. Gray Herb. New Series, no. 49. pp. 79. 1917.

[7] STANDLEY, PAUL C., The Mexican and Central American species of *Ficus*. Contrib. U.S. Nat. Herb. **20**:1–35. 1917.

[8] WERNHAM, H. F., Tropical American Rubiaceae. VIII. Jour. Botany **55**:169–177. 1917.